

11-8-2023

Seasonal Differences in Diet Specialization, Frugivory, and Seed Dispersal in a Subtropical Population of Gopher Tortoise

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

SEASONAL DIFFERENCES IN DIET SPECIALIZATION, FRUGIVORY, AND
SEED DISPERSAL IN A SUBTROPICAL POPULATION OF GOPHER TORTOISE

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

EARTH SYSTEMS SCIENCE

by

Adrian Figueroa

2023

To: Dean Michael R. Heithaus
College of Arts, Sciences and Education

This dissertation, written by Adrian Figueroa, and entitled Seasonal Differences in Diet Specialization, Frugivory, and Seed Dispersal in a Subtropical Population of Gopher Tortoise, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

Steven M. Whitfield

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Date of Defense: November 8, 2023

The dissertation of Adrian Figueroa is approved.

Dean Michael R. Heithaus
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Andrés G. Gil
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and Dean of the University Graduate School

Florida International University, 2023

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DEDICATION

I dedicate this dissertation to my parents Fernando Figueroa and Martha Interian-Figueroa, my brothers Carlos Ferro and Ariel Figueroa, and my girlfriend Amanda Padrón. Mom y Papá, gracias por querer y apoyarme en todos mis esfuerzos. Los quiero con toda mi alma y si no fuera por tu apoyo y tu fe en lo que tus hijos pueden lograr, esta etapa de mi vida no hubiera sido posible. Gracias por poner a nosotros, tus hijos, primero en todo lo que hacen. Las palabras no pueden describir lo agradecido que estoy por sus sacrificios, y por ser su hijo.

Carlos and Ariel, I want to express how lucky I am that you two are my brothers. You have always been there when I have needed you most. When I have gone to you two with my troubles, sometimes all I needed was someone talk to but you guys often eased my worries by reminding me that everything would work out and I would get to where I want to be. Thank you and I love you guys. Let's go Heat!

Amanda, thank you for your love and support through the most difficult of times that many never got to see. No matter how challenging things got for me or how much I sometimes doubted myself, you always believed in me and consoled me when I needed it most. I cannot express how thankful I am for you and your unwavering love and support. I love you.

Lastly, I would like to dedicate this dissertation to the loving memory of Honey, our family dog who passed away on July 5th, 2022, at the age of 19 years old. God only knows how much you were loved. Mom, Papá, Carlos, Ariel, Amanda, y Honey, los quiero con todo mi corazón.

ACKNOWLEDGMENTS

I would like to acknowledge my committee members who have been incredibly helpful over the course of my dissertation. Dr. Joel Heinen's global perspective and expertise in conservation policy has served to highlight the implications of my research for biodiversity conservation and management. Dr. Hong Liu's research on seed dispersal by the Florida box turtles in Big Pine Key was the catalyst for my interest in seed dispersal and pine rockland ecology, and I have been extremely grateful for her support and thoughtful critiques as I refined my dissertation. Dr. Clinton Jenkins' expertise in spatial ecology has helped me realize the implications of my research and the broad application of seed dispersal to the global conservation of biodiversity. Dr. Steven Whitfield has supported my research from the time I was an undergraduate student and continued to provide me with opportunities to continue pursuing this work as a graduate student. Without his guidance and support, I would not have amassed the dataset I did to complete this dissertation nor had the ability to prevail.

I would like to thank experts outside of my committee who lent their expertise in ecology and statistics to help me realize the full potential of my study system: Drs. Pedro Jordano, Mauro Galetti, Márcio Silva Araújo, Kyle Coblenz, Jeferson Vizentin-Bugoni, Brittany Harris, Isabella Ghement, Solomon Kurz, Gavin Simpson, Stephen Wild, Robert Kubinec, Pavel Chernyavskiy, and Michael Greenacre. I would also like to thank my crucial collaborators who helped in scat collection and dissection, and identification of fecal contents: Alyssa Herrera, Lydia Cuni, and Jennifer Villate.

Finally, thank you to the following funders for supporting my graduate school endeavor: NSF Bridge to the Doctorate Fellowship, Zoo Miami Foundation, FIU Institute of Environment Graduate Student Fellowship, FIU DEA Fellowship, and FIU DYF.

ABSTRACT OF THE DISSERTATION

SEASONAL DIFFERENCES IN DIET SPECIALIZATION, FRUGIVORY, AND
SEED DISPERSAL IN A SUBTROPICAL POPULATION OF GOPHER TORTOISE

by

Adrian Figueroa

Florida International University, 2023

Miami, Florida

Professor Joel T. Heinen, Co-Major Professor

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This dissertation is the culmination of a 1.5-year research project into the unique ecology of gopher tortoises (*Gopherus polyphemus*) at the southeasternmost extent of the species' range. This study population occupies the globally imperiled pine rockland ecosystem of Miami-Dade County, Florida, USA, of which >98% no longer exists outside Everglades National Park. My research unveiled a seasonal shift in the diet of the gopher tortoise population where individuals became more specialized in the wet season (June to November) than in the dry season (December to May). This temporal difference in diet specialization coincided with a shift toward frugivory. As frugivory increased, so did diet specialization even after accounting for seasonal effects in the analysis. I subsequently quantified the temporal patterns of frugivory and how different fruit species contributed to the frugivorous diet of the gopher tortoise. Out of the 16 fleshy-fruited plant species consumed, five explained >95% of the variation in frugivory by the tortoises. I then found that as frugivory increased, so did the number of fleshy-fruited species being dispersed, alluding to a potential broadening in the partner plant species

whose seeds the gopher tortoises disperse as they become more frugivorous. Lastly, I used network theory to construct and analyze an intra-specific seed dispersal network and further examined how morphological traits, seasonality, and the endozoochory (i.e., fleshy fruit) dispersal syndrome shape seed dispersal interactions in this population. Carapace length was the strongest predictor for how specialized the tortoises were in their seed dispersal interactions and how diverse their range of partner species were. As carapace length increased, tortoises were more generalized and more diverse in the partner plant species whose seeds they would disperse. Further analyses revealed that wet and dry season networks were very different from one another due to network rewiring, which I confirmed was the result of both seasonality and the dispersal syndrome of fleshy-fruited plants in the network. This demonstrated that the functional role of the gopher tortoise shifts intra-annually to become more frugivorous not only through its diet, but by interacting with and dispersing the seeds of many fleshy-fruited species during the wet season.

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INTRODUCTION

Ecology has a rich history and the development of niche theory – as with other scientific theories – has been built upon the contributions of several important works. Frederic Edward Clements first described the ecological community as a “superorganism” comprised of diverse species acting in concert with one another (Clements, 1916), while Clements’ contemporary Henry Gleason viewed the ecological community as a collection of species who simply shared common habitat requirements (Gleason, 1926). Thereafter, Charles Elton defined the ecological community based on the feeding relationships of species in an ecosystem (Elton, 2001). Suffice it to say that in ecology, diverse ways of viewing the same phenomena have built upon one another to develop this scientific discipline.

Although ecology has expanded and the many subdisciplines within it have flourished in the past 100 years, some inconsistencies have also developed. G. Evelyn Hutchinson’s (1957) conceptualization of a species’ ecological niche, and subsequent advancements of the theory (Colwell & Rangel, 2009), assumed equivalence between conspecific individuals. These developments regarded any variation among individuals within a species to be irrelevant in the context of niche theory. This generalization oversimplified the complexity underpinning ecological systems, as a brief review of Georgy Gause’s competitive exclusion principle quickly reveals the flaw in the assumption of conspecific equivalence. The competitive exclusion principle states that no two identical competitors can coexist in perpetuity (Gause, 1932). If two competitors occupy the same ecosystem, competing for the exact same resources, the competitive exclusion principle – also known as Gause’s law – states that one species will drive the

other to extinction. This is because the superior competitor will exploit resources more efficiently in the ecosystem than the inferior competitor, leading to extinction of the latter. Coexistence of competitors will not be possible unless the inferior competitor can diverge in resource usage from the superior competitor in at least some way.

At the intraspecific level, there is no reason why Gause's law should not operate. Based on Gause's law, the best individual competitor of a species will eliminate other conspecifics if they compete for exactly the same resources within a given habitat. Yet this does not occur in nature, as competing individuals of the same species find ways to coexist. Coexistence can be achieved if conspecific individuals diverge from one other in resource use, behavior, habitat use, or some other plastic trait. This major realization was made by Van Valen in (1965), who first acknowledged the necessity of accounting for individual variation in resource use into the broader discipline of niche theory.

Niche theory has become a paradigm for investigating intraspecific variation in resource use and its implications for community dynamics and ecosystem processes (Chase & Leibold, 2009). This theory provides a framework for understanding how conspecific individuals partition resources in space and time, and how intraspecific competition results in coexistence via niche expansion and individual diet specialization (Araújo et al., 2011; Bolnick, 2001; Bolnick et al., 2007). The relevance of niche theory extends beyond the level of the population or community, as it also has important implications for the functioning of ecosystems (Des Roches et al., 2018).

One area where niche theory can be applied to consider the importance of intraspecific variation, is on ecosystem services through the lens of seed dispersal (Bolnick et al., 2003; Fuster & Traveset, 2020; Zwolak, 2018). Intraspecific phenotypic

variation and subsequent resource use can have considerable impacts on the range of ecosystem services provided by conspecific individuals via seed dispersal (Zwolak, 2018; Zwolak & Sih, 2020). This among-individual variation can result in outcomes anywhere from strongly mutualistic to strongly antagonistic, depending on the nature and strength of the interaction between prospective seed dispersers and the plants they consume (Marques Dracxler & Kissling, 2022; van Leeuwen et al., 2022). One way to quantify how intraspecific variation can affect the process of seed dispersal is through network theory (Bascompte, 2009; Bascompte et al., 2003; Bascompte & Jordano, 2007). This framework provides an empirical lens in which to quantify the impact animals have on the process of seed dispersal via morphological traits and seasonal shifts in diet, allowing for the systematic assessment of the role individuals play in determining seed dispersal interactions.

A relatively new paradigm that merges niche theory – specifically intraspecific resource and trait variation – with seed dispersal ecology, can be found in the Niche Variation Hypothesis (hereafter NVH) literature (Araújo et al., 2008, 2011; Bolnick et al., 2002; Zaccarelli et al., 2013). The niche variation hypothesis posits that populations with wider niches exhibit more intraspecific variation in resource use than populations with narrower niches (Soule & Stewart, 1970). This niche expansion is owed to generalist species being released from interspecific competition – also known as competitive release – and are thus able to exploit a wider range of the resource niche (Bolnick et al., 2007; Svanbäck & Bolnick, 2007). After competitive release, a population of generalists may expand their niche in one of two ways: either (1) all individuals shift their diet to consume a wide range of trophic resources, or (2) all individuals continue using a narrow

range of resources but diverge from one another in order to minimize intraspecific resource competition (Bolnick et al., 2007). In this way, you can quantify proportional similarity in diet, individual specialization, and other resource utilization metrics (Araújo et al., 2008, 2011; Bolnick et al., 2002; Roughgarden, 1972; Zaccarelli et al., 2013). These metrics allow you to examine the relationship between seasonality – for example – and diet specialization, like in the case of species that seasonally become frugivorous (Koike et al., 2008; Remis, 1997).

Subsequently, quantifying which food categories drive diet specialization and how the consumption of these resources varies temporally can provide insight into how these feeding relationships might influence seed dispersal interactions – especially if the food categories driving these phenomena involve seed-bearing plants. The use of network theory can then connect the NVH literature to seed dispersal ecology by linking the drivers of diet specialization to patterns of fruit consumption and seed dispersal. This approach provides a heuristic tool for simultaneously quantifying how temporal factors such as seasonality might drive differences in diet specialization, frugivory, and subsequently the functional role of conspecifics through their role as seed dispersers.

In my dissertation, I provide a three-pronged approach to improve our understanding of individual diet specialization, frugivory, and seed dispersal by employing diverse methods used in the NVH and seed dispersal ecology literature (Balme et al., 2020; Coblenz et al., 2017; Jordano, 2016; Vizentin-Bugoni et al., 2019, 2021). The goal of my dissertation is to expand on foundational ecological concepts to elucidate the importance of individuals in the provisioning of ecosystem services within a globally imperiled ecosystem, the pine rocklands of south Florida.

- In Chapter 1, I calculate indices that quantify the degree of individual diet consistency and specialization across all individuals in the study. I then stratify by seasonality (wet vs. dry season) to test if there are seasonal differences in diet consistency and specialization across the population as well as what food categories drive seasonal patterns in diet composition. Lastly, I test whether frugivory drives diet specialization.
- In Chapter 2, I quantify the population-wide temporal shift toward frugivory and decompose how this cyclical pattern in resource use varies across the four calendar seasons (winter, spring, summer, and fall), while accounting for individual-level variation. I subsequently identify which fleshy-fruit-bearing plants drive fruit consumption in this population, as well as how the dispersal of plant species with the endozoochory syndrome (i.e., fleshy fruit; Ridley, 1930; Van der Pijl, 1982) varies as frugivory increases.
- In Chapter 3, I construct an intraspecific seed dispersal network where I examine network structure and topology both across the entire study and at the seasonal subnetwork level (wet season and dry season). I then examine what individual-level morphological traits shape interaction specialization and partner diversity, as well as the role of seasonality and the endozoochory dispersal syndrome in rewiring the network between the dry season and wet season.

Finally, I conclude my dissertation with new insights gained through my work and explore the implications of this newfound knowledge on the conservation of biodiversity and species interactions in south Florida and abroad.

LITERATURE CITED

- Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, 14(9), 948–958. <https://doi.org/10.1111/j.1461-0248.2011.01662.x>
- Araújo, M. S., Guimarães Jr., P. R., Svanbäck, R., Pinheiro, A., Guimarães, P., Reis, S. F. dos, & Bolnick, D. I. (2008). Network Analysis Reveals Contrasting Effects of Intraspecific Competition on Individual vs. Population Diets. *Ecology*, 89(7), 1981–1993. <https://doi.org/10.1890/07-0630.1>
- Balme, G. A., Roex, N., Rogan, M. S., & Hunter, L. T. B. (2020). Ecological opportunity drives individual dietary specialization in leopards. *Journal of Animal Ecology*, 89(2), 589–600. <https://doi.org/10.1111/1365-2656.13109>
- Bascompte, J. (2009). Mutualistic networks. *Frontiers in Ecology and the Environment*, 7(8), 429–436. <https://doi.org/10.1890/080026>
- Bascompte, J., & Jordano, P. (2007). Plant-animal mutualistic networks: The architecture of biodiversity. *Annual Review of Ecology Evolution and Systematics*, 38, 567–593. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095818>
- Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, 100(16), 9383. <https://doi.org/10.1073/pnas.1633576100>
- Bolnick, D. I. (2001). Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. *Nature*, 410(6827), 463–466.
- Bolnick, D. I., Svanbäck, R., Araújo, M. S., & Persson, L. (2007). Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences*, 104(24), 10075–10079. <https://doi.org/doi:10.1073/pnas.0703743104>
- Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, 161(1), 1–28.
- Bolnick, D. I., Yang, L. H., Fordyce, J. A., Davis, J. M., & Svanbäck, R. (2002). Measuring Individual-Level Resource Specialization. *Ecology*, 83(10), 2936–2941. [https://doi.org/10.1890/0012-9658\(2002\)083\[2936:MILRS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2936:MILRS]2.0.CO;2)
- Chase, J. M., & Leibold, M. A. (2009). Ecological niches. In *Ecological Niches*. University of Chicago Press.
- Clements, F. E. (1916). *Plant succession: An analysis of the development of vegetation* (Issue 242). Carnegie institution of Washington.

- Coblentz, K. E., Rosenblatt, A. E., & Novak, M. (2017). The application of Bayesian hierarchical models to quantify individual diet specialization. *Ecology*, 98(6), 1535–1547. <https://doi.org/10.1002/ecy.1802>
- Colwell, R. K., & Rangel, T. F. (2009). Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences*, 106(supplement_2), 19651–19658. <https://doi.org/10.1073/pnas.0901650106>
- Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., Schweitzer, J. A., & Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, 2(1), 57–64. <https://doi.org/10.1038/s41559-017-0402-5>
- Elton, C. S. (2001). *Animal Ecology* (M. A. Leibold & T. J. Wootton, Eds.). University of Chicago Press. <https://press.uchicago.edu/ucp/books/book/chicago/A/bo25281897.html>
- Fuster, F., & Traveset, A. (2020). Importance of intraspecific variation in the pollination and seed dispersal functions of a double mutualist animal species. *Oikos*, 129(1), 106–116. <https://doi.org/10.1111/oik.06659>
- Gause, G. F. (1932). Experimental Studies on the Struggle for Existence. *Journal of Experimental Biology*, 9(4), 389–402. <https://doi.org/10.1242/jeb.9.4.389>
- Gleason, H. A. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, 7–26.
- Hutchinson, G. E. (1957). Cold spring harbor symposium on quantitative biology. *Concluding Remarks*, 22, 415–427.
- Jordano, P. (2016). Sampling networks of ecological interactions. *Functional Ecology*, 30(12), 1883–1893.
- Koike, S., Kasai, S., Yamazaki, K., & Furubayashi, K. (2008). Fruit phenology of *Prunus jamasakura* and the feeding habit of the Asiatic black bear as a seed disperser. *Ecological Research*, 23(2), 385–392. <https://doi.org/10.1007/s11284-007-0399-3>
- Marques Dracxler, C., & Kissling, W. D. (2022). The mutualism–antagonism continuum in Neotropical palm–frugivore interactions: From interaction outcomes to ecosystem dynamics. *Biological Reviews*, 97(2), 527–553. <https://doi.org/10.1111/brv.12809>
- Remis, M. J. (1997). Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: Use of variable resources. *American Journal of Primatology*, 43(2), 87–109. [https://doi.org/10.1002/\(SICI\)1098-2345\(1997\)43:2<87::AID-AJP1>3.0.CO;2-T](https://doi.org/10.1002/(SICI)1098-2345(1997)43:2<87::AID-AJP1>3.0.CO;2-T)

- Ridley, H. N. (1930). *The dispersal of plants throughout the world*. L. Reeve & Company, Limited.
- Roughgarden, J. (1972). Evolution of Niche Width. *The American Naturalist*, 106(952), 683–718. <https://doi.org/10.1086/282807>
- Soule, M., & Stewart, B. R. (1970). The “Niche-Variation” Hypothesis: A Test and Alternatives. *The American Naturalist*, 104(935), 85–97. <https://doi.org/10.1086/282642>
- Svanbäck, R., & Bolnick, D. I. (2007). Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences*, 274(1611), 839–844. <https://doi.org/doi:10.1098/rspb.2006.0198>
- Van der Pijl, L. (1982). *Principles of dispersal in higher plants* (Vol. 214). Springer.
- van Leeuwen, C. H. A., Villar, N., Mendoza Sagrera, I., Green, A. J., Bakker, E. S., Soons, M. B., Galetti, M., Jansen, P. A., Nolet, B. A., & Santamaría, L. (2022). A seed dispersal effectiveness framework across the mutualism–antagonism continuum. *Oikos*, n/a(n/a), e09254. <https://doi.org/10.1111/oik.09254>
- Van Valen, L. (1965). Morphological Variation and Width of Ecological Niche. *The American Naturalist*, 99(908), 377–390. <https://doi.org/10.1086/282379>
- Vizentin-Bugoni, J., Sperry, J. H., Kelley, J. P., Gleditsch, J. M., Foster, J. T., Drake, D. R., Hruska, A. M., Wilcox, R. C., Case, S. B., & Tarwater, C. E. (2021). Ecological correlates of species’ roles in highly invaded seed dispersal networks. *Proceedings of the National Academy of Sciences*, 118(4), e2009532118. <https://doi.org/10.1073/pnas.2009532118> %J Proceedings of the National Academy of Sciences
- Vizentin-Bugoni, J., Tarwater, C. E., Foster, J. T., Drake, D. R., Gleditsch, J. M., Hruska, A. M., Kelley, J. P., & Sperry, J. H. (2019). Structure, spatial dynamics, and stability of novel seed dispersal mutualistic networks in Hawai‘i. *Science*, 364(6435), 78–82.
- Zaccarelli, N., Bolnick, D. I., & Mancinelli, G. (2013). RInSp: An R Package for the Analysis of Individual Specialization in Resource Use. *Methods in Ecology and Evolution*, 4(11), 1018–1023.
- Zwolak, R. (2018). How intraspecific variation in seed-dispersing animals matters for plants. *Biological Reviews*, 93(2), 897–913. <https://doi.org/10.1111/brv.12377>
- Zwolak, R., & Sih, A. (2020). Animal personalities and seed dispersal: A conceptual review. *Functional Ecology*, 34(7), 1294–1310. <https://doi.org/10.1111/1365-2435.13583>

CHAPTER I. FRUGIVORY DRIVES SEASONAL DIFFERENCES IN DIET
SPECIALIZATION IN A SUBTROPICAL POPULATION OF GOPHER
TORTOISE (*GOPHERUS POLYPHEMUS*)

INTRODUCTION

Individual specialization is the process by which conspecifics diversify their diet when compared to their population and can be caused by a variety of drivers which include competition, predation, and ecological opportunity (Bolnick et al. 2007, Araújo et al. 2011). In some species, as resource diversity increases, so does the degree of diet specialization among individuals (Balme et al. 2020). As different species have different energetic and nutritional demands, their foraging habits can inform which resources may facilitate individual diet specialization.

For example, in the western lowland gorilla (*Gorilla gorilla gorilla*) – a well-documented folivorous great ape (Remis and Dierenfeld 2004) – fruit availability increases, so does its degree of frugivory (Remis 1997). In fact, gorilla movement patterns change seasonally to track the availability of fleshy fruits (Robira et al. 2023). Furthermore, different foraging groups of gorillas have been found to differ in their fruit consumption – providing insight into the pivotal role that fruit resources may play in facilitating diet specialization for opportunistic frugivores (Fuh et al. 2022). However, individual diet specialization has not been formally quantified for this species.

Frugivory is not only a foraging strategy, but a crucial ecological interaction (Jordano 2000, Jordano et al. 2011). Fruit consumption represents a transaction where animals meet their energetic and nutritional needs (Herrera 2002), and plants receive the dispersal services of their offspring (Traveset et al. 2014). Between 60 to 80% of all plant

species benefit from seed dispersal via ingestion and excretion through animals (Levey et al. 2002, Dennis 2007), which results in the production of various consumptive resources and ecosystem services (Forget et al. 2011, Bello et al. 2015).

While seed dispersal research has traditionally considered the effects of animal dispersers at the species level, studies are beginning to suggest examining the importance of conspecifics for the process of animal-mediated seed dispersal (Zwolak 2018, Zwolak and Sih 2020). Understanding how diet specialization varies among conspecifics and what role frugivory may have in facilitating this process provides a first step towards better understanding how both individual specialization and patterns of frugivory may influence seed dispersal.

In this study, I aimed to address three overarching questions: 1) What are the patterns of intra and inter individual diet specialization among conspecific herbivores? 2) Are there seasonal shifts in the degree of individual diet specialization? and 3) Does frugivory play a role in driving diet specialization in an opportunistic frugivore?

I hypothesized that: 1) There are marked differences in how consistent individual diets are, and how specialized individuals are when compared to the rest of the population, 2) In seasons with greater resource availability – such as the fruiting season – there will be greater intra and inter individual diet specialization, and 3) As fruit consumption increases in primarily herbivorous fauna, so does their degree of diet specialization.

METHODS

1.1. Site Description

This study took place in Miami-Dade County, Florida, USA, in the globally imperiled pine rockland ecosystem (USFWS 1999, Florida Natural Areas Inventory 2010, World Wildlife Fund 2014). Specifically, this work was conducted at an 830-ha complex of properties known as The Richmond Tract (Possley et al. 2020, Figueroa et al. 2023), in the rocklands surrounding Zoo Miami which serves as critical habitat for numerous endemic and federally listed species, as well as the population of gopher tortoises (*Gopherus polyphemus*) under study here (Possley et al. 2018, Whitfield et al. 2018, 2022, Figueroa et al. 2021). Southern Florida, where the pine rockland forests are located, has a subtropical climate where seasonal fluctuations in temperature are less pronounced than that of rainfall (Snyder et al. 1990, Lodge 2017). Here, summer and fall are considered the wet season (June to November) and winter and spring the dry season (December to May) (Snyder et al. 1990, Lodge 2017). As a result, the phenology of many plants in this community coincides with these seasonal changes in precipitation.

The pine rockland is the most floristically diverse ecosystem in southern Florida, containing over 430 plant species (Trotta et al. 2018), many of which are endemic to this region and ecosystem type. Its biotic community represents the confluence of temperate species at the southern extent of their geographic range and neotropical species at the northern extent of theirs. This ecosystem is fire-maintained and characterized by its scant, savanna-like canopy of endemic South Florida slash pine (*Pinus elliottii* var. *densa*), midstory of palms and shrubs, and understory of endemic, fire-dependent herbs such as Florida brickell-bush (*Brickellia mosieri*), Carter's small-flowered flax (*Linum carteri*

carteri), and deltoid spurge (*Euphorbia deltoidea* ssp. *deltoidea*) (Possley et al. 2008, Diamond and Heinen 2016). In addition to the diversity of plants they contain, pine rocklands provide habitat for a longtime inhabitant of this ecosystem that persists in remnant preserves to this day, the gopher tortoise (Simpson 1920, Carr 1940, Monroe 1943, Enge et al. 2004, Whitfield et al. 2018, 2022, Figueroa et al. 2021).

1.2. Study Species

The gopher tortoise is the only native tortoise found east of the Mississippi and Tombigbee rivers (Auffenberg and Franz 1982), and has been documented as southeast as Miami, Florida by early homesteaders (Simpson 1920, Monroe 1943), and at Cape Sable in the 1980s – which is at the southwestern tip of the Florida peninsula (Kushlan and Mazzotti 1984, Waddle et al. 2006). Gopher tortoises are widely recognized for their proclivity to burrow, supporting over 350 commensal species (Diemer 1986, Lips 1991, Dziadzio and Smith 2016, Melanson 2021), and are primarily herbivorous (MacDonald and Mushinsky 1988, Mushinsky et al. 2003). This species is known to forage on upwards of 1,000 plant species across its range (Ashton and Ashton 2008), and although an efficient herbivore (Bjorndal 1987), the gopher tortoise also engages in frugivory – acting as a prolific seed disperser (Carlson et al. 2003, Birkhead et al. 2005, Hanish 2018, Richardson and Stiling 2019, Figueroa et al. 2021). On occasion, this species will also scavenge, engage in coprophagy, and consume rocks and shells as gastroliths (Moore and Dornburg 2014, Yuan et al. 2015). Due to their broad diet, this species provides a good model for investigating individual variation in resource-use patterns, particularly in the floristically diverse south Florida pine rockland ecosystem (Trotta et al. 2018).

The tortoises at the study site have been the subject of multiple studies regarding ecology and conservation (Whitfield et al. 2018, 2022, Figueroa et al. 2021), and are found in three disjunct spatial aggregations which I refer to as the East, South and West sites (Fig. I.1). These aggregations of tortoises are due to a combination of the species' social behavior (Guyer et al. 2012), as well as the geology of this ecosystem which can limit the availability of deep sandy soils that facilitate burrowing (Hoffmeister et al. 1967, Whitfield et al. 2022). During the study, no tortoises migrated from one of these aggregations to another, so each site has a perfectly nested subset of individuals that occupy it.

Vegetatively, the plant communities in the West, South, and East sites are very similar where they fall within the pine rockland footprint. However, half of the burrows in the East aggregation were surrounded by invasive plant species such as Burma reed (*Neyraudia reynaudiana*), showy rattlebox (*Crotalaria spectabilis*), shrub verbena (*Lantana camara*), and bitter melon (*Momordica charantia*) just outside the pine rockland footprint (Fig. I.1). Although there are contrasts in the plant communities inside and outside the pine rockland footprint, the estimates of individual diet specialization are calculated across the entire population of tortoises over the whole study period, thereby incorporating spatial and temporal differences in diet specialization into the population average.

1.3. Study Design

Scat Collection/Dissection

This study was carried out over a 1.5-year period with scat collection beginning on May 11th, 2021, and ending on November 9th, 2022. I used radio telemetry to track wild gopher tortoises at The Richmond Tract twice weekly. If an individual tortoise defecated during handling, the fecal sample would be collected in a plastic bag and labeled with the tortoise's ID number, location, and date encountered.

Scats were dissected with forceps over laminated graph paper (29.59cm x 21.01cm), containing 5mm x 5mm grids as a static background reference to compare the relative contributions of food items to the total fecal volume. All food items recovered from the fecal sample were identified to the lowest taxonomic unit or qualified as their own category (e.g., fur/hair was recovered from multiple species and subsequently categorized jointly). After dissection, fecal contents were spread over the laminated graph paper and the relative contributions of each food item to the total scat volume was visually estimated; an approach widely used in dietary studies (Klare et al. 2011).

Food item contributions were quantified as proportions of either 0.01, 0.05, or in increments of 0.05 all the way to the total scat volume of 1.00. If values less than 0.05 remained after quantifying the contributions of all food items, this amount was allocated to the most abundant food category from the sample. Of all the plant species consumed, only seeds and undigested pulp from endozoochorous (fleshy-fruited) species were considered as "fruit" in the sample (Ridley 1930, Van der Pijl 1982). While running oak (*Quercus pumila*) fruits (i.e., acorns) lack a fleshy mesocarp, I included them in the fruit

category since acorns are usually sought after for consumption, even by turtles (Carlson et al. 2003, Elbers and Moll 2011).

Aggregating Food Categories

Food items were ultimately aggregated into the following five functional food categories due to their distinct importance in gopher tortoise diets (Bjorndal 1987, MacDonald and Mushinsky 1988, Ashton and Ashton 2008, Moore and Dornburg 2014, Figueroa et al. 2021):

1. Grasses were all members of the plant family Poaceae.
2. Legumes were all members of the plant family Fabaceae.
3. Other Plants were an aggregation of all other plant material that did not qualify as Legumes or Grasses yet were part of the vegetative aspect of the tortoise diet.
4. Fruit represents all endozoochorous fruits consumed by gopher tortoises, following dispersal syndromes from classical literature in seed dispersal ecology (Ridley 1930, Van der Pijl 1982).
5. Lastly, the Animals category captures all material that is of animal origin (e.g., snail shells, eggshells, bone, and mammal fur).

The motive for aggregating food items in this way rather than using the taxonomic classification of each food item was to reduce the dimensionality of the dataset while maintaining enough resolution to examine how different functional groups contribute to shifts in dietary composition as well as individual specialization (Newsome et al. 2015).

1.4. Statistical Analysis

All statistical analyses were carried out in R version 3.3.0 (R Core Team 2022).

1.4.1. Bayesian Hierarchical Modeling

To quantify intra- and inter-individual diet specialization, I employed the Bayesian hierarchical modeling framework implemented by Coblenz et al. (2017) in the `rjags` package (Plummer et al. 2016). This approach models the proportions in each of the food categories within each sample and at higher hierarchical levels such as individuals and populations. Briefly, the proportions of each food category in the diet samples are modeled following a multinomial distribution which required scaling the proportions to lie between 0 and 100. The sample proportions are then assumed to follow a Dirichlet distribution at the next highest hierarchical level (here for example the individual from which the sample was taken) (see Coblenz et al. 2017 for modeling details).

Quantifying Individual Consistency and Specialization

To calculate intra- and inter-individual diet specialization, I specified a hierarchical model with samples nested within the individuals of origin. I then calculated the Proportional Similarity of samples (PS_{si}), which describes how similar the composition of a sample s is to the mean of all samples provided by individual i :

$$(1) \quad PS_{si} = 1 - 0.5 \sum_j |p_{ij} - q_{ij}|$$

where p_{ij} is the contribution of food item j in a sample of individual i , while q_{ij} is the contribution of food item j in the overall diet of individual i , as long as the individual provided more than one fecal sample in the dataset.

To quantify the amount of intra-individual diet specialization in the population, I first calculated the mean PS_{si} from all the samples belonging to individual i (N_{si}) [Equation (2)]. I refer to this metric as Individual Consistency (IC_i).

$$(2) \quad IC_i = \frac{\sum_{si}(PS_{si})}{N_{si}}$$

An IC_i close to 0.00 indicates very low similarity between an individual's fecal samples and its overall dietary composition. On the other hand, an IC_i close to 1.00 indicates that samples are very close to the overall dietary composition of individual i , hence a more consistent diet.

For inter-individual diet specialization, I calculated the sample-level proportional similarity to the population diet (PS_s), which quantifies how similar an individual's samples are to the population diet [Equation (3)].

$$(3) \quad PS_s = 1 - 0.5 \sum_j |p_{ij} - q_j|$$

p_{ij} is the contribution of food item j in a sample of individual i and q_j is the contribution of food item j to the diet of the whole population. Like for PS_{si} , PS_s values were only calculated for individuals that provided more than one fecal sample.

Additionally, I estimated Individual Specialization (IS_i) like in IC_i [Equation (4)], by calculating the mean of all PS_s values across the number samples provided by each tortoise (N_{si}).

$$(4) \quad IS_i = \frac{\sum_i(PS_s)}{N_{si}}$$

An IS_i value close to 0.00 indicates low similarity between an individual's samples and the whole population whereas a value closer to 1.00 indicates high similarity between individual's samples and the whole population.

To calculate the IC_i and IS_i values of all individuals, I ran the model on the full dataset and extracted the posterior draws for all individuals (14 individuals; 180 fecal samples total). I then plotted the posterior draws with the 95% Credible Intervals for each individual. This approach allowed us to robustly quantify the consistency in diet of various individuals as well as their degree of individual resource use specialization (see Bolnick et al. 2002, Zaccarelli et al. 2013, and Coblenz et al. 2017 for more detail on the calculation of these metrics).

Quantifying Temporal Differences in Diet Consistency and Specialization

After quantifying individual consistency and specialization for each tortoise in the population, I then ran the same model specification on two subsets of the full dataset: one containing only wet season samples and one containing only dry season samples. I subsequently extracted the PS_{si} and PS_s values for all samples in each season and plotted their posterior estimates together. This allowed us to examine seasonal differences in the sample-level measures of diet consistency and specialization, respectively.

To examine differences in PS_{si} and PS_s across seasons, I subtracted the posterior draws of both PS_{si} and PS_s between the wet and dry season. This allowed us to quantify the differences in sample-level diet consistency and specialization between seasons. For all estimates, I calculated the Bayesian probability of direction (PD) from the posterior distribution (Makowski et al. 2019). PD can be interpreted as the probability that the median of the estimate is strictly positive or negative, depending on which is most probable. This was done by dividing the number of posterior draws demonstrating the

effect of interest (i.e., negative or positive values indicating the directionality of the effect), by the total number of posterior draws.

1.4.2. Correspondence Analysis to Characterize Spatiotemporal Shifts in Dietary Composition

To quantify whether and how dietary composition varied between the wet and dry seasons, I performed a Correspondence Analysis in the easyCODA package (Greenacre 2017, 2019). This multivariate analysis pinpoints which food categories contribute most to the composition of fecal samples across seasons, allowing us to gauge how food categories contribute to observed shifts in diet, and potentially individual consistency and specialization.

I performed the Correspondence Analysis to visualize how diets varied seasonally and then overlaid vectors that illustrate the magnitude of influence for each of the five food categories on the diet composition. Lastly, I drew 95% confidence ellipses for each level of season, ultimately resulting in a Discriminant Correspondence Analysis. I quantified the influence of each food category on the total dietary composition by calculating the inertia captured by each in the Correspondence Analysis.

After the Correspondence Analysis, I used the vegan package to perform Permutational Analyses of Variance (PERMANOVA) on the Bray-Curtis dissimilarity matrix of the original dataset (Oksanen et al. 2022). This allowed us to assess significant differences in the population diet composition between seasons.

1.4.3. GLMM for Influence of Frugivory on Diet Specialization

Lastly, I used the Bayesian brms package (Bürkner 2017) to construct a Generalized Linear Mixed Model (GLMM) which modeled the mean posterior estimates of PS_{si} and PS_s as the response variables to test if frugivory drove intra and inter individual diet specialization, respectively. Given that PS_{si} and PS_s lie between 0.00 and 1.00, I specified a beta error distribution for both models with an uninformative prior. The estimates for PS_{si} and PS_s used as the response variable came from the two subsets of the full dataset used to calculate sample-level consistency and specialization in the wet and dry seasons. As the fixed effects, I specified an interaction between the proportion of fecal volume comprised of fruit and the season in which samples were collected. I then included a random effect to account for differences among individuals, inherently capturing spatial differences due to the nested nature of the tortoises across the three sites. Finally, I plotted the relationship between frugivory and individual consistency, as well as specialization, while stratifying by season to account for seasonal differences in the relationship.

RESULTS

Individual tortoises varied greatly in their consistency IC_i and specialization IS_i , with individuals who were more inconsistent in their foraging patterns also more specialized when compared to the population (Fig. I.2). On the other hand, individuals that exhibited greater diet consistency exhibited less specialization. When plotting PS_{si} and PS_s values by season, a clear seasonal pattern in both diet consistency and specialization emerged (Fig. I.3). In the wet season, diets were much more inconsistent

and specialized than in the dry season, with a median difference in consistency of -0.11, and in specialization of -0.13, with neither of the credible intervals overlapping with 0.00. The PD estimate for the wet and dry season contrasts in both consistency and specialization was 100%. This indicated a high probability that diets in the wet season are both more inconsistent and specialized than in the dry season.

The Correspondence Analysis subsequently demonstrated that fruit consumption primarily explained the differences in dietary composition between the dry and wet seasons (Fig. I.4), with fruit containing the highest inertia value of 0.54 compared to the other food categories which all fell below 0.35 (Table I.1). PERMANOVA results confirmed that diets differed significantly in their composition in the wet season compared to the dry season, with a p-value of 3.60E-05 (F-value = 17.859; df1 = 1; df2 = 205).

Modeling the relationship between fruit consumption and both sample-level diet consistency and specialization revealed a clear negative relationship (Fig. I.5). As diets became more frugivorous, they also became more specialized and more inconsistent with the rest of an individual's fecal samples (Table I.2). The effect of frugivory alone had the strongest effect among the fixed effects and their interactions for both models. In the sample-level diet consistency model, frugivory had a PD value of 98.44% while in the sample-level diet specialization model, the PD value was 99.02%. Similar, seasonality had a high PD value in both models (>95%), but the PD for the interaction between seasonality and frugivory were not as high in either, but still considerable (~80%). These results demonstrate that frugivory plays a major role in driving dietary inconsistency and

specialization, even after accounting for individual variation through the random effect term.

DISCUSSION

In the present study, I explored the temporal nature of quantifying diet specialization (Novak and Tinker 2015, Rosenblatt et al. 2015), to compare how different individual diets were intra-annually, finding that in the two distinct south Florida seasons, wet and dry, there were marked differences in intra and inter individual specialization. I documented substantial inter-individual variation in the individual-level estimates of dietary consistency (IC_i) and specialization (IS_i), where individuals with more varied diets also demonstrated more specialized diets when compared to the population. I then observed inter-seasonal differences in the sample-level measures of dietary consistency (PS_{si}) and specialization (PS_s), with more varied and specialized diets in the wet season than dry season, confirming that specialization is greater with increased precipitation as has been found in desert tortoises (*Gopherus agassizii*) (Murray and Wolf 2013).

Dietary composition itself also varied inter-seasonally, with frugivory contributing most to this shift. Modeling sample-level diet consistency and specialization as a function of the interaction between season and frugivory – while accounting for individual-tortoise variation – revealed that frugivory is a major driver of both levels of diet specialization (i.e., intra individual diet consistency and inter individual diet specialization). As frugivory increased, irrespective of season, so did the variability of an individual's fecal samples when compared to its total diet, as well as how specialized the individual was when compared to the population.

Although not explicitly quantified here, I suspect that frugivory increases intra-annually as precipitation brings with it greater fruit availability, and that individual gopher tortoises seek out these resources as they become increasingly available in time. As mentioned earlier, previous studies have found that the folivorous western lowland gorilla becomes more frugivorous seasonally by tracking the spatiotemporal availability of fleshy fruits (Remis 1997, Robira et al. 2023). This seasonal tracking of fruits allows the gorillas to incorporate more digestible energy and a greater abundance of macronutrients into their diet (Masi et al. 2015). With the western lowland gorilla being a hindgut fermenter (Remis and Dierenfeld 2004) – like the gopher tortoise (Bjorndal 1987) – it is able to extract a great amount of energy from fibrous food items. Although adequate energy could be obtained without fruit, the digestive similarities between the gorilla and the gopher tortoise suggest that the readily available carbohydrates and digestible energy in fruit could allow for more time in the gopher tortoise’s activity budget to copulate (Johnson et al. 2007), defend or expand home ranges (McRae et al. 1981, Masi et al. 2009), and burrow during periods of high fruit consumption (Eubanks et al. 2003). The timing of these documented behaviors in the gopher tortoise coincides with greater fruit consumption and specialization by the tortoises investigated herein.

These results demonstrate that temporally, the gopher tortoise engages in opportunistic frugivory that facilitates diet specialization through increased intra-individual diet variation. This notion suggests that rather than falling in any one category between herbivory or frugivory (van Leeuwen et al. 2022), species – or individuals – may shift their diets to increase their consumption of temporally-limited resources such as fruit (Abrahms et al. 2021), thereby allowing them to specialize their diets. The

ramifications of these findings are that individuals may engage in different degrees of frugivory and seed dispersal as they become increasingly specialized, suggesting that conspecifics can provide unique seed dispersal services through diet specialization rather than through morphological or behavioral differences alone (Zwolak 2018, Zwolak and Sih 2020), although they may be related.

By unraveling the temporal differences in individual diet specialization that is driven by frugivory, this research contributes to the understanding of the mechanisms shaping ecological dynamics at the intraspecific level that can subsequently influence community-level interactions such as frugivory and seed dispersal (Zwolak 2018, Marques Dracxler and Kissling 2022, van Leeuwen et al. 2022). Such insights have implications for conservation and management efforts, as they can identify vulnerable populations lacking the appropriate resource diversity for their maintenance and can inform the ways in which habitat management can facilitate their persistence. Moreover, a comprehensive understanding of individual specialization provides a foundation for predicting responses to environmental perturbations and enhances the ability to conserve biodiversity in the face of global change. I encourage future studies that quantify how the consumption of resources that facilitate diet specialization, such as frugivory, varies temporally and what the subsequent implications are for the seed dispersal services provided.

TABLES

Seasonal Correspondence Analysis Results					
Food Category	Mass	ChiDist	Inertia	Dim. 1	Dim. 2
Fruit	0.101836	2.293578	0.535707	-2.939796	-0.40552
Animals	0.037826	2.954706	0.330233	0.18281	2.347988
Legumes	0.14599	1.498334	0.327749	0.010057	2.021206
Other Plants	0.067923	1.890907	0.24286	0.374998	-0.047709
Grasses	0.646425	0.491206	0.155972	0.410755	-0.524971

Table I.1. Summary table for the Correspondence Analysis. Food categories are ordered from highest to lowest Inertia, which is the amount of variance captured by the food category. "Mass" refers to the total frequency of observations associated with a category while "ChiDist" measures the chi-squared dissimilarity between categories based on observed and expected frequencies, aiding in the calculation of distances in the low-dimensional representation of the data. "Dim. 1" and "Dim. 2" are the principal coordinate values for each category.

Summary Table for Effect of Frugivory and Seasonality on PS_{si} and PS_s					
Metric	Variable	Lower 95% CI	Median Estimate	Upper 95% CI	PD
PS _{si}	Frugivory	-4.977	-2.501	-0.237	98.44%
PS _{si}	Season	-0.426	-0.199	0.020	96.14%
PS _{si}	Frugivory:Season	-1.397	0.853	3.342	76.56%
PS _s	Frugivory	-5.222	-2.732	-0.417	99.02%
PS _s	Season	-0.479	-0.269	-0.058	99.38%
PS _s	Frugivory:Season	-1.370	0.938	3.459	79.24%

Table I.2. Summary table for the effect of frugivory and seasonal differences on the sample-level measures of diet consistency (PS_{si}) and specialization (PS_s). Posterior median estimates, lower 95%, and upper 95% credible intervals (CI) are displayed in log-odds, along with the probability of direction (PD) for the estimates.

FIGURES

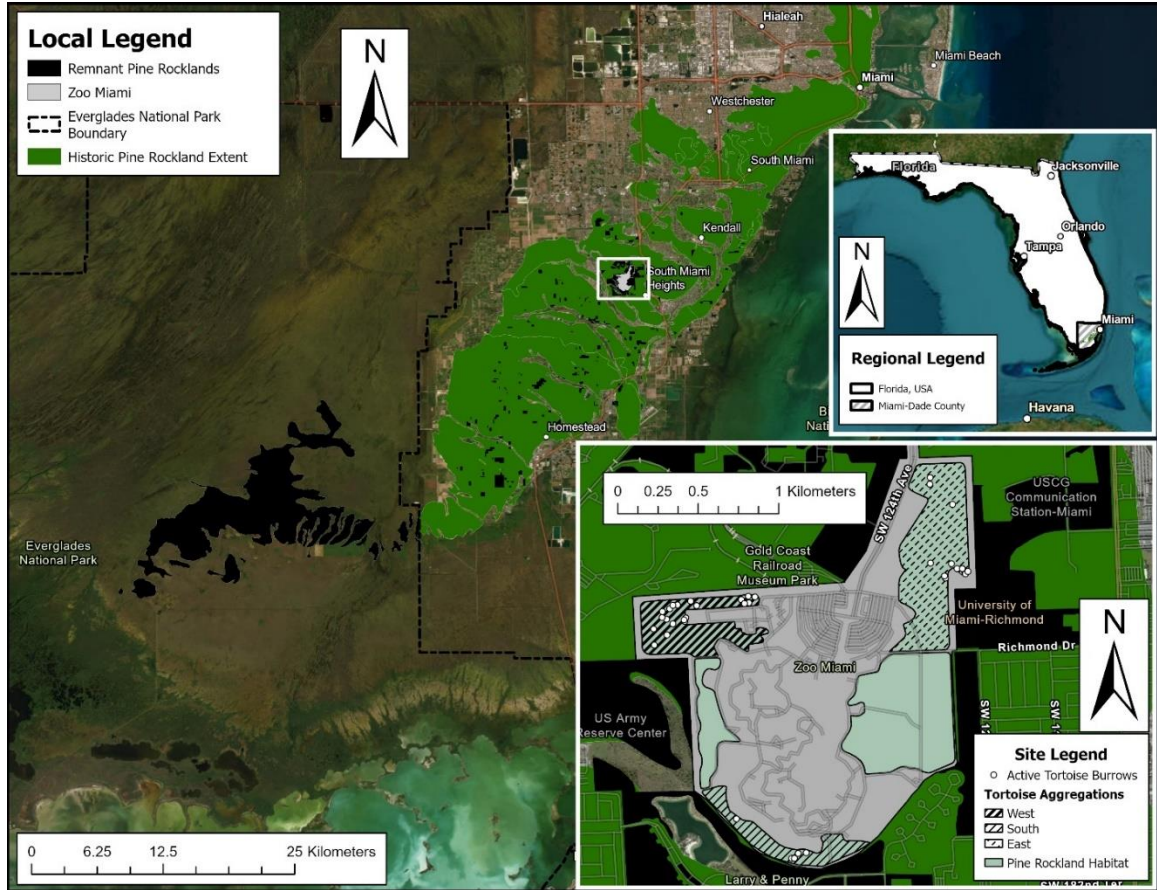


Figure I.1. The study site, Zoo Miami, lies on the largest expanse of pine rockland habitat outside of Everglades National Park, known as The Richmond Tract in Miami-Dade County, Florida, USA.

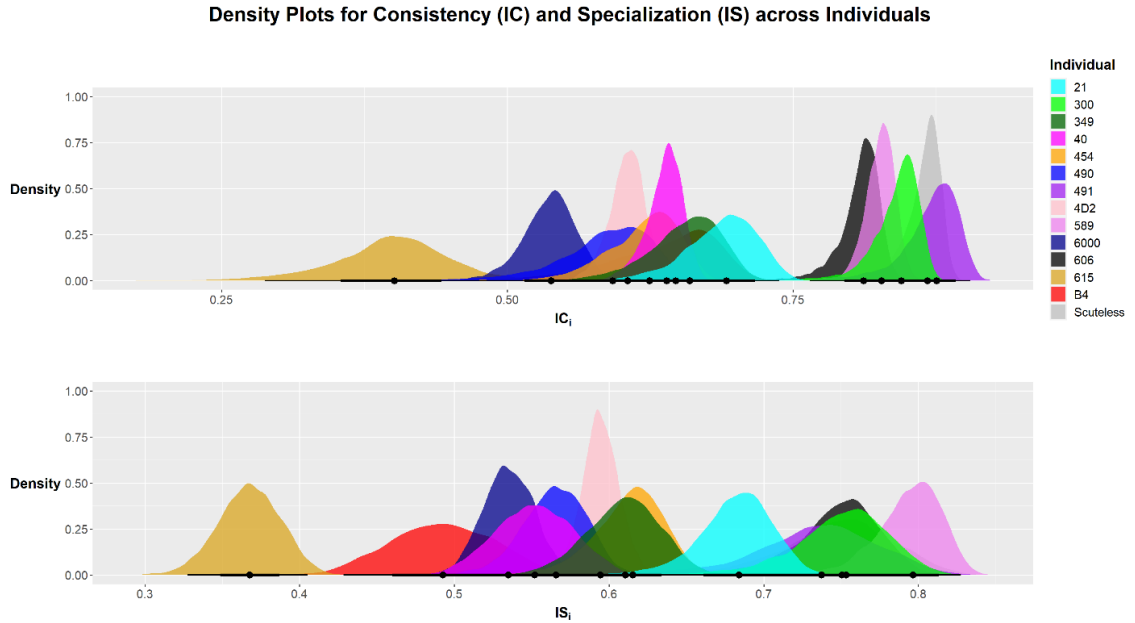


Figure I.2. Individual-level measures of diet consistency (IC_i ; top panel) and specialization (IS_i ; bottom panel) across all tortoises in the study that provided more than one fecal sample. Values closer to 0.00 indicate greater inconsistency/specialization whereas values closer to 1.00 indicate greater consistency and less specialization.

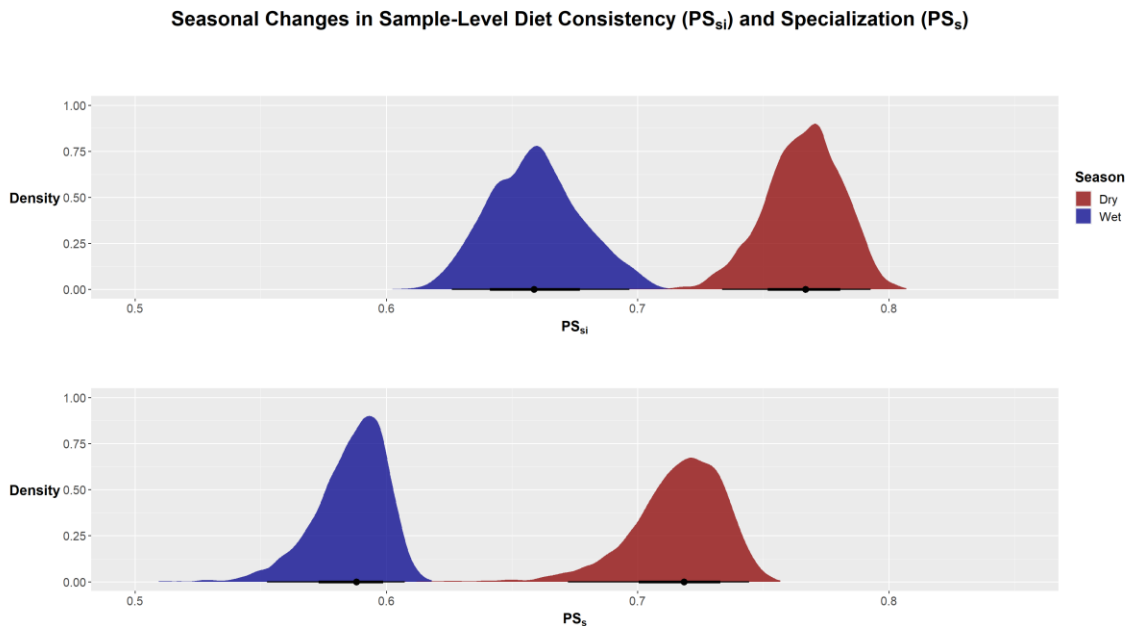


Figure I.3. Density plots illustrating seasonal shifts in sample-level measures of diet consistency (PS_{si} ; top panel) and specialization (PS_s ; bottom panel). Values closer to 0.00 indicate greater inconsistency/specialization whereas values closer to 1.00 indicate greater consistency and less specialization.

Between-Season Discriminant Correspondence Analysis (DCA)

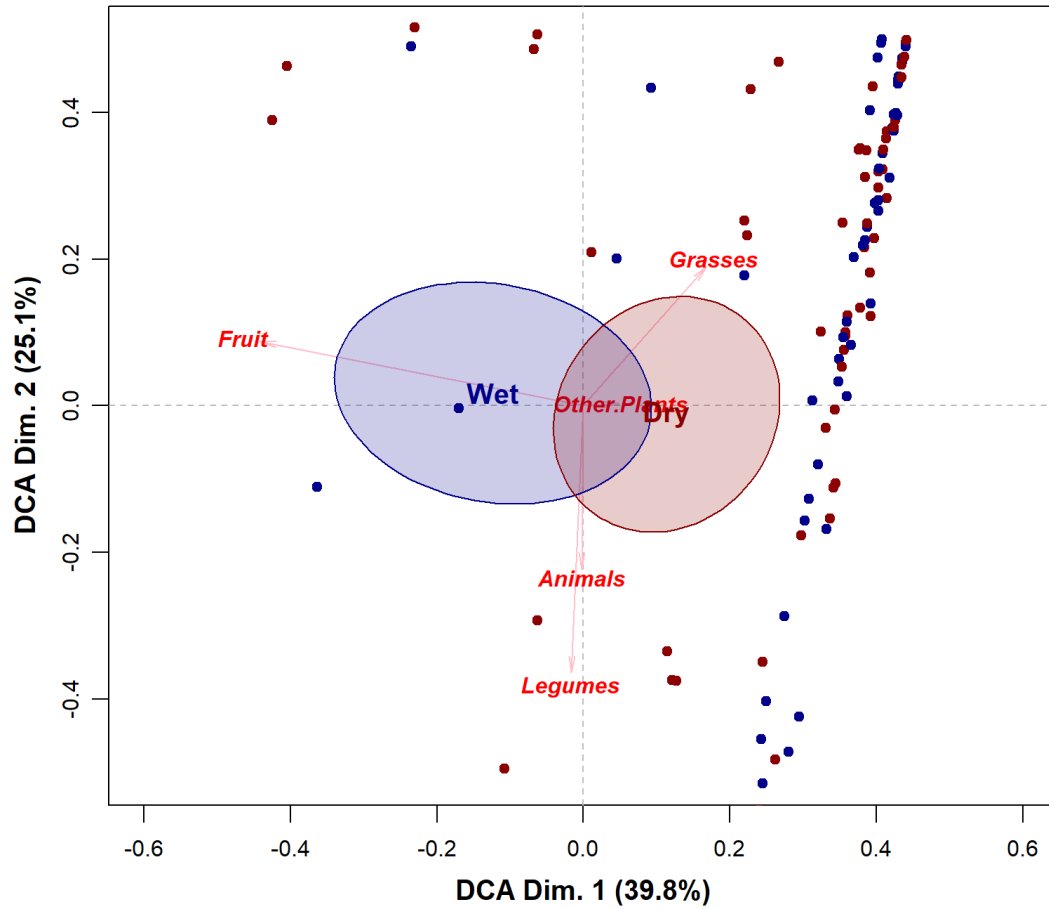


Figure I.4. Discriminant Correspondence Analysis depicting seasonal shifts dietary composition, with 95% confidence ellipses around each season. Wet season is blue and Dry season is red.

Changes in Sample-Level Diet Consistency (PS_{si}) and Specialization (PS_s) as Fruit Consumption Increases

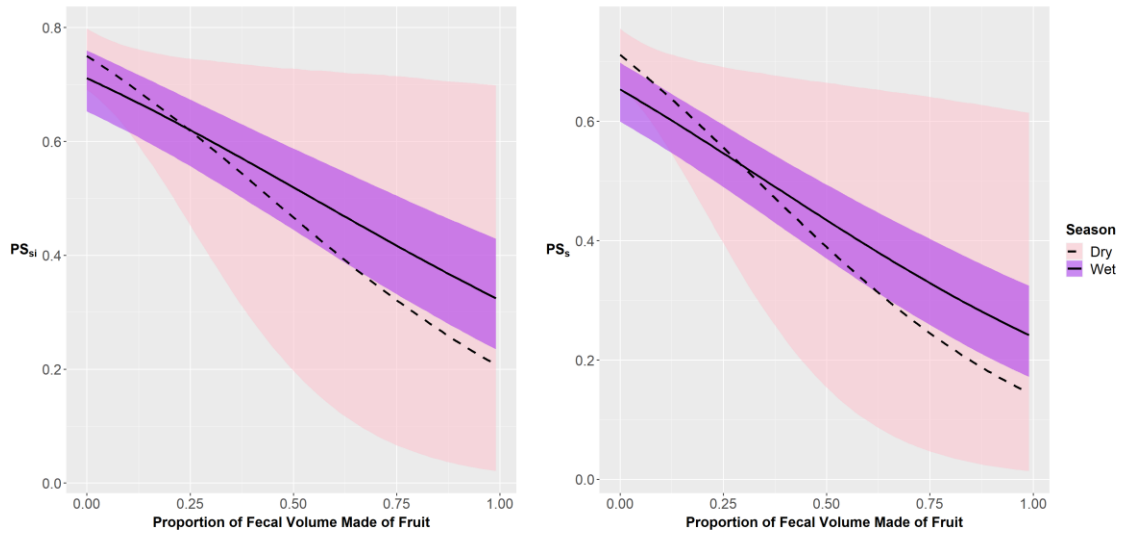


Figure I.5. Regression plots from the Generalized Linear Mixed Models, illustrating the influence of frugivory on sample-level diet consistency (PS_{si} ; left panel) and specialization (PS_s ; right panel). Values closer to 0.00 indicate greater inconsistency/specialization whereas values closer to 1.00 indicate greater consistency and less specialization.

LITERATURE CITED

- Abrahms, B., E. O. Aikens, J. B. Armstrong, W. W. Deacy, M. J. Kauffman, and J. A. Merkle. 2021. Emerging Perspectives on Resource Tracking and Animal Movement Ecology. *Trends in Ecology & Evolution* 36:308–320.
- Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. *Ecology Letters* 14:948–958.
- Ashton, R. E., and P. S. Ashton. 2008. The Natural History and Management of the Gopher Tortoise. *Gopherus polyphemus*:65–93.
- Auffenberg, W., and R. Franz. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). *North American Tortoises: Conservation Ecology*:95–126.
- Balme, G. A., N. Roex, M. S. Rogan, and L. T. B. Hunter. 2020. Ecological opportunity drives individual dietary specialization in leopards. *Journal of Animal Ecology* 89:589–600.
- Bello, C., M. Galetti, M. A. Pizo, L. F. S. Magnago, M. F. Rocha, R. A. F. Lima, C. A. Peres, O. Ovaskainen, and P. Jordano. 2015. Defaunation affects carbon storage in tropical forests. *Science Advances* 1:e1501105.
- Birkhead, R. D., C. Guyer, S. M. Hermann, and W. K. Michener. 2005. Patterns of folivory and seed ingestion by gopher tortoises (*Gopherus polyphemus*) in a southeastern pine savanna. *American Midland Naturalist* 154:143–151.
- Bjorndal, K. A. 1987. Digestive Efficiency in a Temperate Herbivorous Reptile, *Gopherus polyphemus*. *Copeia* 1987:714–720.
- Bolnick, D. I., R. Svanbäck, M. S. Araújo, and L. Persson. 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences* 104:10075–10079.
- Bolnick, D. I., L. H. Yang, J. A. Fordyce, J. M. Davis, and R. Svanbäck. 2002. Measuring Individual-Level Resource Specialization. *Ecology* 83:2936–2941.
- Bürkner, P.-C. 2017. brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software* 80:1–28.
- Carlson, J. E., E. S. Menges, and P. L. Marks. 2003. Seed dispersal by *Gopherus polyphemus* at Archbold Biological Station, Florida. *Florida Scientist* 66:147–154.
- Carr, A. F. 1940. Contribution to the herpetology of Florida.

- Coblentz, K. E., A. E. Rosenblatt, and M. Novak. 2017. The application of Bayesian hierarchical models to quantify individual diet specialization. *Ecology* 98:1535–1547.
- Dennis, A. J. 2007. Seed dispersal: theory and its application in a changing world. CABI.
- Diamond, J. M., and J. T. Heinen. 2016. Conserving rare plants in locally-protected urban forest fragments: A case study from Miami-Dade County, Florida. *Urban Forestry & Urban Greening* 20:1–11.
- Diemer, J. E. 1986. The Ecology and Management of the Gopher Tortoise in the Southeastern United States. *Herpetologica* 42:125–133.
- Dziadzio, M. C., and L. L. Smith. 2016. Vertebrate use of gopher tortoise burrows and aprons. *Southeastern Naturalist* 15:586–594.
- Elbers, J. P., and D. Moll. 2011. Ingestion by a Freshwater Turtle Alters Germination of Bottomland Hardwood Seeds. *Wetlands* 31:757–761.
- Enge, K. M., M. S. Robson, and K. L. Krysko. 2004. Reptile surveys of pine rockland habitat in six Miami-Dade County parks. *Florida Scientist* 67:194–204.
- Eubanks, J. O., W. K. Michener, and C. Guyer. 2003. Patterns of movement and burrow use in a population of gopher tortoises (*Gopherus polyphemus*). *Herpetologica* 59:311–321.
- Figuroa, A., J. T. Heinen, F. N. Ridgley, S. M. Whitfield, and H. Liu. 2023. Management of a Globally Imperiled and Fire-Dependent Ecosystem in the Urban Matrix of Miami–Dade County, Florida: A Case Study of the Richmond Tract Pine Rocklands. *Diversity* 15:426.
- Figuroa, A., J. Lange, and S. M. Whitfield. 2021. Seed Consumption by Gopher Tortoises (*Gopherus polyphemus*) in the Globally Imperiled Pine Rockland Ecosystem of Southern Florida, USA. *Chelonian Conservation and Biology* 20:27–34, 8.
- Florida Natural Areas Inventory. 2010. Guide to the Natural Communities of Florida.
- Forget, P.-M., P. Jordano, J. E. Lambert, K. Böhning-Gaese, A. Traveset, and S. J. Wright. 2011. Frugivores and seed dispersal (1985–2010); the ‘seeds’ dispersed, established and matured. *Acta Oecologica* 37:517–520.
- Fuh, T., A. Todd, A. Feistner, G. Donati, and S. Masi. 2022. Group differences in feeding and diet composition of wild western gorillas. *Scientific Reports* 12:9569.
- Greenacre, M. 2017. Correspondence Analysis in Practice. Chapman and Hall/CRC.
- Greenacre, M. 2019. Package ‘easyCODA.’ *Compositional Data Analysis in Practice* 35.

- Guyer, C., V. M. Johnson, and S. M. Hermann. 2012. Effects of Population Density On Patterns of Movement and Behavior of Gopher Tortoises (*Gopherus polyphemus*). *Herpetological Monographs* 26:122–134.
- Hanish, C. J. 2018. Seed Dispersal of the Cocoplum (*Chrysobalanus icaco*) by Gopher Tortoises (*Gopherus polyphemus*) in Southeastern Florida. Florida Atlantic University.
- Herrera, C. M. 2002. Seed dispersal by vertebrates. *Plant–animal interactions: an evolutionary approach*:185–208.
- Hoffmeister, J. E., K. W. Stockman, and H. G. Multer. 1967. Miami Limestone of Florida and its recent Bahamian counterpart. *Geological Society of America Bulletin* 78:175–190.
- Johnson, V. M., C. Guyer, and M. D. Boglioli. 2007. Phenology of Attempted Matings in Gopher Tortoises. *Copeia* 2007:490–495.
- Jordano, P. 2000. Fruits and frugivory. *Seeds: the ecology of regeneration in plant communities* 2:125–166.
- Jordano, P., P.-M. Forget, J. E. Lambert, K. Böhning-Gaese, A. Traveset, and S. J. Wright. 2011. Frugivores and seed dispersal: mechanisms and consequences for biodiversity of a key ecological interaction. *Biology Letters* 7:321–323.
- Klare, U., J. F. Kamler, and D. W. MacDonald. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review* 41:294–312.
- Kushlan, J. A., and F. J. Mazzotti. 1984. Environmental Effects on a Coastal Population of Gopher Tortoises. *Journal of Herpetology* 18:231–239.
- van Leeuwen, C. H. A., N. Villar, I. Mendoza Sagraera, A. J. Green, E. S. Bakker, M. B. Soons, M. Galetti, P. A. Jansen, B. A. Nolet, and L. Santamaría. 2022. A seed dispersal effectiveness framework across the mutualism–antagonism continuum. *Oikos*:e09254.
- Levey, D. J., W. R. Silva, and M. Galetti. 2002. *Seed dispersal and frugivory: ecology, evolution, and conservation*. CABI.
- Lips, K. R. 1991. Vertebrates Associated with Tortoise (*Gopherus polyphemus*) Burrows in 4 Habitats in South-Central Florida. *Journal of Herpetology* 25:477–481.
- Lodge, T. E. 2017. *The Everglades Handbook: Understanding the Ecosystem (Fourth Edition)*. Everglades Handbook: Understanding the Ecosystem, 4th Edition.

- MacDonald, L. A., and H. R. Mushinsky. 1988. Foraging Ecology of the Gopher Tortoise, *Gopherus polyphemus*, in a Sandhill Habitat. *Herpetologica* 44:345–353.
- Makowski, D., M. S. Ben-Shachar, S. H. A. Chen, and D. Lüdecke. 2019. Indices of Effect Existence and Significance in the Bayesian Framework. *Frontiers in Psychology* 10:2767.
- Marques Dracxler, C., and W. D. Kissling. 2022. The mutualism–antagonism continuum in Neotropical palm–frugivore interactions: from interaction outcomes to ecosystem dynamics. *Biological Reviews* 97:527–553.
- Masi, S., C. Cipolletta, and M. M. Robbins. 2009. Activity patterns of western lowland gorillas (*Gorilla gorilla gorilla*) at Bai-Hokou, Central African Republic. *Am J Prim* 71:91–100.
- Masi, S., R. Mundry, S. Ortmann, C. Cipolletta, L. Boitani, and M. M. Robbins. 2015. The Influence of Seasonal Frugivory on Nutrient and Energy Intake in Wild Western Gorillas. *PLOS ONE* 10:e0129254.
- McRae, W. A., J. L. Landers, and J. A. Garner. 1981. Movement Patterns and Home Range of the Gopher Tortoise. *The American Midland Naturalist* 106:165–179.
- Melanson, L. 2021. Investigating vertebrate relationships of the south Florida gopher tortoise: a study of vertebrate species within scrub, pine rockland, coastal hammock and grassland habitats. Florida Atlantic University.
- Monroe, M. B. 1943. Pioneer Women of Dade County. *Tequesta* 1:54–55.
- Moore, J. A., and A. Dornburg. 2014. Ingestion of Fossil Seashells, Stones and Small Mammal Bones by Gravid Gopher Tortoises (*Gopherus polyphemus*) in South Florida. *Bulletin of the Peabody Museum of Natural History* 55:55–63, 9.
- Murray, I. W., and B. O. Wolf. 2013. Desert Tortoise (*Gopherus agassizii*) Dietary Specialization Decreases across a Precipitation Gradient. *Plos One* 8:e66505.
- Mushinsky, H. R., T. A. Stilson, and E. D. McCoy. 2003. Diet and dietary preference of the juvenile gopher tortoise (*Gopherus polyphemus*). *Herpetologica* 59:475–483.
- Newsome, S. D., M. T. Tinker, V. A. Gill, Z. N. Hoyt, A. Doroff, L. Nichol, and J. L. Bodkin. 2015. The interaction of intraspecific competition and habitat on individual diet specialization: a near range-wide examination of sea otters. *Oecologia* 178:45–59.
- Novak, M., and M. T. Tinker. 2015. Timescales alter the inferred strength and temporal consistency of intraspecific diet specialization. *Oecologia* 178:61–74.

- Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, and P. Solymos. 2022. *vegan: Community Ecology Package*. R package version 2.5-7. 2020.
- Plummer, M., A. Stukalov, and M. Denwood. 2016. *rjags: Bayesian graphical models using MCMC*. R package version 4.
- Possley, J., J. Duncan, J. Gil, and C. Grossenbacher. 2020. Too Precious To Lose: Managing and Protecting the Richmond Pine Rockland Tract (Richmond) in Miami Dade County, South Florida. *Cities and the Environment* 13.
- Possley, J., J. Duncan, J. Klein, and J. Maguire. 2018. Miami-Dade County's Management Plan for the Richmond Pine Rocklands, 2nd ed. Prepared by Fairchild Tropical Botanic Garden for Miami-Dade County, Department of Parks, Recreation and Open Spaces and Zoo Miami 2:136.
- Possley, J., S. W. Woodmansee, and J. Maschinski. 2008. Patterns of Plant Composition in Fragments of Globally Imperiled Pine Rockland Forest: Effects of Soil Type, Recent Fire Frequency, and Fragment Size. *Natural Areas Journal* 28:379–394.
- R Core Team. 2022. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Remis, M. J. 1997. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: Use of variable resources. *American Journal of Primatology* 43:87–109.
- Remis, M. J., and E. S. Dierenfeld. 2004. Digesta Passage, Digestibility and Behavior in Captive Gorillas Under Two Dietary Regimens. *International Journal of Primatology* 25:825–845.
- Richardson, J. C., and P. Stiling. 2019. Gopher Tortoise (*Gopherus polyphemus*) Gut Passage Can Alter Seed Germinability. *The American Midland Naturalist* 182:181–190.
- Ridley, H. N. 1930. *The dispersal of plants throughout the world*. L. Reeve & Company, Limited.
- Robira, B., S. Benhamou, T. N. Fuh, and S. Masi. 2023. Do Seasonal Frugivory and Cognition Shape Foraging Movements in Wild Western Gorillas? Pages 151–170 in R. Reyna-Hurtado, C. A. Chapman, and M. Melletti, editors. *Movement Ecology of Afrotropical Forest Mammals*. Springer International Publishing, Cham.
- Rosenblatt, A. E., J. C. Nifong, M. R. Heithaus, F. J. Mazzotti, M. S. Cherkiss, B. M. Jeffery, R. M. Elsey, R. A. Decker, B. R. Silliman, L. J. Guillette, R. H. Lowers, and J. C. Larson. 2015. Factors affecting individual foraging specialization and

- temporal diet stability across the range of a large “generalist” apex predator. *Oecologia* 178:5–16.
- Simpson, C. T. 1920. In lower Florida wilds:174–184.
- Snyder, J. R., A. Herndon, and W. B. Robertson Jr. 1990. South Florida Rockland. *Ecosystems of Florida*:230–277.
- Traveset, A., R. Heleno, and M. Nogales. 2014. The Ecology of Seed Dispersal. *Seeds: The Ecology of Regeneration in Plant Communities*, 3rd Edition:62–93.
- Trotta, L. B., B. Baiser, J. Possley, D. J. Li, J. Lange, S. Martin, and E. B. Sessa. 2018. Community phylogeny of the globally critically imperiled pine rockland ecosystem. *American Journal of Botany* 105:1735–1747.
- USFWS. 1999. Pine Rocklands Management Plan.
- Van der Pijl, L. 1982. Principles of dispersal in higher plants. Springer.
- Waddle, J. H., F. J. Mazzotti, and K. G. Rice. 2006. Changes in Abundance of Gopher Tortoise Burrows at Cape Sable, Florida. *Southeastern Naturalist* 5:277–284, 8.
- Whitfield, S. M., F. N. Ridgley, D. Valle, and N. Atteberry. 2018. Seroprevalence of *Mycoplasma agassizii* and *Mycoplasma testudineum* in Wild and Waif Gopher Tortoises (*Gopherus polyphemus*) in Miami-Dade County, Florida, USA. *Herpetological Review* 49:47–49.
- Whitfield, S. M., D. Valle, A. Figueroa, B. Chin, H. Bravo-Gallegos, and F. Leone. 2022. Burrow Characteristics and Habitat Associations of Gopher Tortoises in Urban Pine Rockland Reserves (Miami, Florida, USA). *Ichthyology & Herpetology* 110:22–32.
- World Wildlife Fund. 2014. South Florida rocklands.
- Yuan, M. L., S. H. Dean, A. V. Longo, B. B. Rothermel, T. D. Tuberville, and K. R. Zamudio. 2015. Kinship, inbreeding and fine-scale spatial structure influence gut microbiota in a hindgut-fermenting tortoise. *Molecular Ecology* 24:2521–2536.
- Zaccarelli, N., D. I. Bolnick, and G. Mancinelli. 2013. RInSp: an R Package for the Analysis of Individual Specialization in Resource Use. *Methods in Ecology and Evolution* 4:1018–1023.
- Zwolak, R. 2018. How intraspecific variation in seed-dispersing animals matters for plants. *Biological Reviews* 93:897–913.
- Zwolak, R., and A. Sih. 2020. Animal personalities and seed dispersal: A conceptual review. *Functional Ecology* 34:1294–1310.

CHAPTER II. TEMPORAL SHIFTS IN FRUGIVORY ACROSS A SUBTROPICAL
POPULATION OF GOPHER TORTOISE (*GOPHERUS POLYPHEMUS*):
IMPLICATIONS FOR SEED DISPERSAL

INTRODUCTION

Resource utilization is a fundamental ecological process that mediates a variety of interactions, from mutualisms to antagonisms (Bronstein 2015). Investigating resource use patterns provides insight into the trophic niche species occupy and the functional roles they may play in an ecosystem (Elton 2001, Chase and Leibold 2009, van Leeuwen et al. 2022). Furthermore, quantifying spatiotemporal patterns in resource use can reveal the consistency of consumers in their dietary habits or shifts toward preferred food items that are limited in time and/or space (Abrahms et al. 2021). One spatiotemporally limited resource that is closely tracked by animals is fleshy fruit (Koike et al. 2008, Takahashi et al. 2008). In many ecosystems, as fleshy fruits become more abundant through time, animals shift their diet to become more frugivorous (Remis 1997, Gerardo Herrera M. et al. 2008, Robira et al. 2023).

Consequently, differences in a consumer's strength of frugivory may influence its effectiveness as a seed disperser (Marques Draxler and Kissling 2022, van Leeuwen et al. 2022), and since seed dispersal is a fundamental aspect in the life cycle of plants (Traveset et al. 2014), the strength of a consumer's frugivory may have implications for plant life histories. Thus, quantifying the importance of fruit in the diet of an animal is a first step toward understanding its dispersal effectiveness (sensu Schupp 1993, Schupp et al. 2010). Identifying which fruit species are important in the consumer's diet then opens the question about the reciprocal importance of the consumer as its disperser. While it has

been demonstrated that plant dispersal syndromes are unreliable in predicting ingestion and dispersal (i.e., endozoochorous dispersal) of seeds (Green et al. 2021), an approach to quantify whether the functional role of an animal seed disperser changes as it becomes more frugivorous is to gauge if seed dispersal for species with the endozoochory syndrome (i.e., fleshy fruit) increases with frugivory.

In this study, I investigated patterns of frugivory in a population of hindgut fermenters, the gopher tortoise (*Gopherus polyphemus*), and aim to address whether its functional role as a seed disperser changes as it becomes more frugivorous. Specifically, I aim to answer the following questions: (1) Are there temporal patterns of frugivory in this species? and (2) Which fleshy fruits drive frugivory? (3) Does the dispersal of species with the endozoochory syndrome increase as frugivory increases?

I hypothesized that after the seasonal precipitation begins, there will be a time lag between peak precipitation and peak frugivory in the gopher tortoise. Considering the phenology of many fleshy fruits in south Florida, coinciding with seasonal rains (Lodge 2017, Flora of North America Editorial Committee, eds. 1993+ 2023), as well as the two-to-three week gut retention time of the gopher tortoise (Bjorndal 1987), I anticipated that frugivory will increase steadily in throughout the summer with its peak in late summer/early fall. I expected that ultimately, the tortoises will disperse more fleshy-fruit species as they become more frugivorous, given the extremely broad and opportunistically frugivorous diet of this species (Ashton and Ashton 2008). This would demonstrate a shift along the mutualism-antagonism continuum by ecologically functioning as a frugivore by dispersing more species with the endozoochory syndrome as fruit consumption increases (sensu van Leeuwen et al. 2022).

METHODS

2.1. Site Description

This study was conducted in the globally imperiled pine rockland ecosystem at The Richmond Tract (Possley et al. 2018, 2020), in Miami-Dade County, Florida, USA (USFWS 1999, Florida Natural Areas Inventory 2010, World Wildlife Fund 2014). The Richmond Tract is a complex of properties that spans 830-ha and contains the largest extent of pine rockland outside of Everglades National Park (Bradley and Gann 2005, Figueroa et al. 2023). The globally imperiled pine rockland ecosystem is the most biodiverse in south Florida, with over 430 native plant species and a multitude of large vertebrates that have been largely extirpated as a result of urbanization and development in the region (Lodge 2017, Trotta et al. 2018).

This ecosystem is fire-maintained and characterized by its scant, savanna-like canopy of endemic South Florida slash pine (*Pinus elliottii* var. *densa*), understory of palms (e.g., *Coccothrinax argentata*, *Sabal palmetto*, *Serenoa repens*) and shrubs which include locustberry (*Byrsonima lucida*), West Indian lilac (*Miconia bicolor*), and pineland croton (*Croton linearis*). Interspersed between the understory, rare and endemic herbs comprise the groundcover layer along with grasses, euphorbs, and succulents like the eastern prickly pear cactus (*Opuntia austrina*) (Possley et al. 2008, Diamond and Heinen 2016). In addition to the diversity of plants they contain, pine rocklands provide habitat for several state and federally listed fauna (USFWS 1999). One of these animals is the gopher tortoise – a longtime inhabitant of the pine rockland ecosystem that persists

in remnant preserves to this day (Simpson 1920, Carr 1940, Monroe 1943, Enge et al. 2004, Whitfield et al. 2018, 2022, Figueroa et al. 2021).

2.2. Study Species

The gopher tortoise is the only native tortoise found east of the Mississippi River (Auffenberg and Franz 1982, Bury and Germano 1994, Edwards et al. 2016). Its range spans the southeastern United States, from Louisiana to South Carolina and south into Miami-Dade County and Cape Sable in Florida (Kushlan and Mazzotti 1984, Enge et al. 2004, Waddle et al. 2006). Gopher tortoises support over 350 commensal animal species that use their burrows (Diemer 1986, Lips 1991) and are known to forage on over 1000 plant species across their range (Ashton and Ashton 2008).

Many studies have investigated the diet and foraging ecology of this species (McRae et al. 1981, MacDonald and Mushinsky 1988, Mushinsky et al. 2003, Ashton and Ashton 2008), classifying it as an herbivore that engages in frugivory (Birkhead et al. 2005, Hanish 2018, Richardson and Stiling 2019a, 2019b). As such, it is a widely-recognized seed disperser by ingesting the seeds of fleshy-fruited (Hanish 2018, Richardson and Stiling 2019a), and “foliage is the fruit” species (Carlson et al. 2003, Birkhead et al. 2005, Figueroa et al. 2021), oftentimes enhancing seed germination (Falcón et al. 2020). The tortoises in this study serve as a model for investigating how frugivory might fluctuate in a seed-dispersing herbivore (Marques Dracxler and Kissling 2022, van Leeuwen et al. 2022), providing an opportunity to quantify which fleshy fruits are an important part of its diet, and whether its functional role as a seed disperser changes temporally.

The tortoises in the study site are found in three aggregations which I refer to as the East, South, and West sites – named after the cardinal directions in which they are located across Zoo Miami’s pine rocklands (see Fig. I.1). These tortoise aggregations are due to a combination of the species’ social behavior (Guyer et al. 2012), as well as the geology of this ecosystem (Hoffmeister et al. 1967), which can limit the availability of deep sandy soils that facilitate burrowing (Whitfield et al. 2022). During the study, no tortoises migrated from one site to another, as I regularly tracked individuals via radio telemetry, so each site has a perfectly nested subset of individuals that occupy it. While formal surveys were not conducted, the plant communities in both the South and West sites were representative of healthy pine rockland while the East site had a greater presence of invasive plant species such as Burma reed (*Neyraudia reynaudiana*), showy rattlebox (*Crotalaria spectabilis*), and shrub verbena (*Lantana camara*).

2.3. Study Design

Scat Collection and Dissection

I conducted this study over a 1.5-year period with scat collection beginning on May 11th, 2021, and ending on November 9th, 2022. I tracked wild gopher tortoises at the Richmond Tract twice weekly via radio telemetry. If an individual defecated during handling, I collected the sample labeled it with the tortoise’s ID number, location, and the date. Sometimes, I encountered fresh fecal samples belonging to unknown tortoises and thus collected them. For these samples, I GPS marked, dated, and labeled them with a unique identifier that indicated it came from an unknown individual.

Fecal samples were either dissected on the same day of collection or frozen for dissection at a future date. I performed scat dissections with forceps over laminated graph paper (29.59cm x 21.01cm) containing 5mm x 5mm grids as a static background reference, and I used this background reference to compare the relative contributions of food items to the total fecal volume. All food items recovered from fecal samples were identified to the lowest taxonomic unit or qualified as their own category (e.g., fur/hair was recovered from multiple species and subsequently categorized as mammal fur).

After dissecting fecal samples and separating contents over the laminated graph paper, I then visually estimated the relative contributions of each food category to the total scat volume was; this approach has been compared with other methods resulting in its acceptance for dietary studies (Klare et al. 2011). I quantified the contribution of five functional food categories – Grasses, Legumes, Other Plants, Fruit, and Animals – to the total fecal volume as either 0.01, 0.05, or in increments of 0.05 all the way to the total scat volume proportion of 1.00. If a value less than 0.05 remained after quantifying the relative contribution of all food items, I would allocate the amount to the most abundant food category in the sample.

Additionally, I identified all seeds extracted from fecal samples to the lowest taxonomic unit using dichotomous keys, online references, and consultations with local botanists (Gann et al. 2001, 2002, Wunderlin et al. 2016). Seeds were then counted and the dispersal syndromes were recorded using criteria from Ridley (1930) and Van der Pijl (1982) to distinguish species with the endozoochory syndrome from all other syndromes (Table II.1).

Quantifying the Strength of Frugivory through Time

While other studies have used activity budgets to quantify the strength of frugivory (Pavelka and Knopff 2004), I directly measured the proportion of total fecal volume comprised of fruit. This measure was used as the response variable in all subsequent analyses on frugivory. As the predictor variables, I used indices of time in the form of calendar days to cover the whole calendar year and in a separate analysis, I used an interaction term between the season in which the sample was collected with the number of days elapsed within that season.

2.4. Statistical Analysis

All statistical analyses were carried out in R version 3.3.0 using various packages that are explicitly stated in the following subsections (R Core Team 2022).

2.4.1. GAMM for Intra-annual Shift Toward Frugivory

I used a Generalized Additive Mixed Model (GAMM) in this analysis to investigate the non-linear shift toward frugivory throughout the calendar year, as outlined by Pedersen et al. (2019). For this purpose, I employed the `ordbetareg` package (Kubinec 2022), which acts as a wrapper for the Bayesian `brms` package (Bürkner 2017, 2018, 2021). I decided on this combination of a GAMM with the `ordbetareg` package because of the combined suitability for handling the zero-inflated, ordered, and proportional characteristics of the response variable. Ordered beta regressions, like the one I applied here, enabled us to model relationships between the lower bound (0), upper bound (1),

and the continuous proportions in between without overfitting the model to the data (Kubinec 2022).

To investigate nonlinearity in frugivory over the calendar year, I specified the calendar day in which samples were collected as the smooth predictor with the response variable representing the proportion of fecal volume attributed to fruit. This approach allowed us to visualize frugivory patterns over time. To account for variability in frugivory among individuals and sites, I introduced a random effect that represented the individual providing each sample. Since individuals were nested entirely within the three sites, the site-level variances were inherently captured in the individual tortoise random effect terms, simplifying the model.

2.4.2. GLMM for Temporal Patterns of Frugivory

Since GAMMs lack interpretability (Wood 2006, Pedersen et al. 2019), I then fitted another ordered beta regression but as a Generalized Linear Mixed Model (GLMM), also in the `ordbetareg` package (Kubinec 2022). To perform this analysis, I first defined each season based on the solstices and equinoxes in each year of the study; 2021 and 2022. I then specified frugivory as a function of the interaction between days elapsed within a season and the season of interest. I also included a random effect to account for differences among individuals and sites, as in the GAMM. The GLMM allowed us to quantify overall differences in fruit consumption between sites and seasons, while allowing us to estimate the rate of change in frugivory within seasons.

For all estimates, I calculated the Bayesian probability of direction (PD) from the posterior distribution (Makowski et al. 2019), which is as a measure of the probability

that the effect is indeed in the observed direction (i.e., positive or negative). This was done by dividing the number of posterior draws in the direction of the posterior median estimate (i.e., negative or positive values indicating the directionality of the effect), by the total number of posterior draws.

2.4.3. LRA and PCA to Determine Contribution of Species to Fruit Diet

To identify which fleshy-fruited species contribute most to the fruit diet of the gopher tortoise, I used Logratio Analysis (LRA). LRA is a compositional data analysis approach that identifies the subset of fruit species responsible for the majority of variance in the dataset (Greenacre 2018, 2019, 2021). I applied this approach to determine which of the 16 fleshy fruit species (Table II.1), contribute most to frugivory by the gopher tortoises. LRA has been employed in ecological studies (Graeve and Greenacre 2020), demonstrating its power in identifying important categories driving biological processes.

To perform this analysis, I created a data frame containing all fecal samples – including those from unknown individuals, as this analysis is conducted at the sample- rather than individual-level. I then excluded all samples containing no fruit from further analysis, since I was interested in which species contributed to observed frugivory. For each of the 16 columns, I then imputed the zero values by half the minimum non-zero value for that species in the whole dataset (Graeve and Greenacre 2020). This zero-value imputation is common practice in compositional data analysis and is needed to perform the LRA (Greenacre 2018, 2019). Lastly, I renormalized the dataset by dividing each cell by the sum of all values in its row (Greenacre 2021).

This final dataset was then ordinated through the LRA to visualize which of the 16 fruit species were major contributors to the variance in frugivory. Inertia values – which represent the variance captured by each category – indicated which fleshy fruits were independently the most variance-explaining. However, I wanted to identify the subset of all fleshy fruits that together explained most of the frugivory rather than simply selecting the single most variance-explaining species from the LRA summary table.

As a result, I next performed stepwise logratio selection to explain the greatest variability in frugivory with each additional logratio selected (see Greenacre 2019b, Graeve and Greenacre 2020 for details). In this iterative process, there were initially 120 logratios to select from, but I did not always select simply the most variance-explaining logratio. In some cases, I selected logratios that explained a great deal of variation and, in addition, made biological sense. For example, fruits of taxonomy, size, or color associated with frugivory in chelonians were prioritized if they were also nearly as variance-explaining as the top logratios (Falcón et al. 2020). This is because chelonians are known to seek out and forage on fruit based on sensory cues, especially those of certain taxa such as palms (Grant 1960, Marques Dracxler and Kissling 2022). The reason for this user input is to “bake in” biological information into the variable selection process to account for variability in an ecologically meaningful way. Ultimately, I stopped selecting logratios once I accounted for > 95% of the variance in gopher tortoise frugivory. In the end, I was left with a short list of endozoochorous species comprising the logratios responsible for most of the frugivory exhibited by the tortoises.

Finally, I used Principal Component Analysis (PCA) to ordinate the logratios selected in the stepwise LRA. The PCA quantified how much variance the selected

logratios captured altogether when compared to the LRA. To estimate how well the selected logratios performed in accounting for variation in frugivory from the full dataset, I calculated the Procrustes correlation between the LRA principal coordinates and the PCA principal coordinates as in Graeve and Greenacre (2020). The Procrustes correlation, along with its significance, indicated whether the selected subset of logratios in the PCA explained a great deal of frugivory in the tortoises as in the LRA.

2.4.4. GLMM for Dispersal of Endozoochorous Species

Lastly, I fitted another GLMM, but this time with the response variable being the number of species with the endozoochory syndrome dispersed as frugivory increased. As a result, I specified a negative binomial error distribution and subsequently calculated the median, lower 95%, and upper 95% credible intervals for the slope values, as well as the PD to determine whether dispersal for species with the endozoochory syndrome increases with frugivory.

RESULTS

2.5. GAMM for Intra-annual Shift Toward Frugivory

After fitting the GAMM, I noted a temporal shift in frugivory by plotting the resulting spline (i.e., nonlinear curve) over a color-coded background representing the seasons (Fig. II.1). As a visual representation of how precipitation also varied interannually, I fitted a spline for the observed rainfall over the calendar year using precipitation data from a nearby meteorological station <4km from the study site.

The spline illustrated that frugivory begins in the late spring, increases substantially over the summer – reaches its peak in the late summer/early fall – and declines gradually throughout the fall, eventually near zero in winter and early/mid spring. The 95% credible intervals emphasize that fruit consumption in summer and fall is substantially greater than zero, differing from that of winter and spring, where their credible intervals are much closer to zero throughout the seasons (Fig. II.1). On the other hand, the peak in frugivory captured in the 95% credible interval in late summer/early fall shows that the proportion of fecal volume comprised of fruit ranges between 0.11 and 0.43, with a median estimate of 0.22.

2.6. GLMM for Temporal Patterns of Frugivory

To quantify temporal patterns of frugivory in greater detail, I fitted the GLMM and created a four-panel regression plot where fruit consumption in each season was depicted and color-coded to match the spline (Fig. II.2). Frugivory increases in the spring and summer before declining in fall and then winter, confirming the GAMM results. Overall, frugivory in summer and fall was much greater than 0.00 while in spring and winter it hovered near 0.00.

2.6.1. Overall Difference in Frugivory Between Seasons

Comparing the strength of frugivory in spring, summer, and fall to that of the winter reference level resulted in stark contrasts (Fig. II.3). There was much greater frugivory in summer and fall than winter while on the other hand, spring and winter did not differ from one another. Summer fecal samples had 0.13 more of their total volume

(1.00) comprised of fruit compared to winter whereas fall had 0.15 more (Table II.2). Meanwhile, spring overlapped strongly with zero when contrasted to the winter level, indicating little to no difference (Table II.2). The PD values for the summer-winter and fall-winter contrasts were both 100% whereas the PD for the spring-winter contrast was 64%, indicating there is likely no difference in frugivory between spring and winter.

2.6.2. Within-Season Changes in Frugivory

After quantifying differences in frugivory among seasons, I then calculated the rate of change in frugivory within each season. These estimates represent the per-month change in frugivory within each season while controlling for site and individual-level effects. While Fig. II.2 illustrates the per-day change in fruit consumption, I multiplied the back transformed slope estimates by a value of 30 to interpret the rate of change more clearly, at the monthly scale (Table II.3). In spring, the median slope estimate was 0.03 whereas in summer it was 0.08. On the other hand, slope estimates for fall and winter were -0.07 and -0.05, respectively, with their monthly changes in frugivory representing a 0.07-unit decrease in fall and a 0.05-unit decrease in winter (Table II.3). Winter, spring, and summer all have PD values above 95%, while fall has a PD of 86.29%, indicating that the within-season relationships are likely to be in the directions estimated, albeit not as strong as in the other seasons.

2.7. LRA and PCA to Determine Contribution of Species to Fruit Diet

The total logratio variance in the frugivory dataset was 0.53, which is based on the total possible combinations of 120 ratios formed by the 16 endozoochorous plant

species. These 16 species are listed in Table II.4 as a summary Table II. of the LRA, quantifying the chi squared distance, inertia, and LRA dimension values for each of the species, in descending order by inertia. These inertia values suggest that individually, saw palmetto, sabal palm, prickly pear, and locustberry are among the most variance-explaining fruits consumed by the tortoises.

To identify which logratios in the dataset best explain the majority of total logratio variance, I followed the stepwise approach of Graeve and Greenacre (2020). The subsequent series of four steps identified five logratios comprised of six fleshy-fruited species that explained 96.96% of the total logratio variance. After these four steps, the addition of more logratios had minimal statistical and practical relevance (Supp. Table II.1).

In the LRA, I consecutively accounted for more of the total logratio variance until I described > 95% of the variance, proceeding with each step as follows:

Step 1: Silver Palm (*Coccothrinax argentata*)/Saw Palmetto (*Serenoa repens*) Ratio

The top 10 logratios all contained saw palmetto, with the first logratio selected comprised of silver palm/saw palmetto, alone accounting for 80.97% of the total logratio variance. This was the sixth most variance-explaining logratio and was selected because of the taxonomic similarity between the species, since both silver palm and saw palmetto are in the Arecaceae family – a family whose fruits are known to be heavily foraged by chelonians (Liu et al. 2004, Platt et al. 2009, Falcón et al. 2020, Figueroa et al. 2021). The leading logratio was comprised of mouse’s pineapple (*Morinda royoc*) with saw palmetto, but it only accounted for 0.48% more of the total variance.

Step 2: Sabal Palm (*Sabal palmetto*)/Saw Palmetto Ratio

In the second step, the top 10 logratios either contained sabal palm or saw palmetto. The logratio pair that was therefore selected on the basis of total logratio variance explained – as well as their biological relatedness as palms – was sabal palm/saw palmetto, accounting for an additional 8.57% of the total logratio variance. This logratio was tied for second on the list, only preceded by mouse’s pineapple which only explained 0.02% more of the total variance.

Step 3: Eastern Prickly Pear (*Opuntia austrina*)/Saw Palmetto Ratio

As in all the previous ratios, saw palmetto explained a large amount of variation when paired with other fleshy fruited species. As a result, this next ratio, eastern prickly pear/saw palmetto accounted for an additional 4.61% of the total logratio variance and led the top 10 logratios as the most variance-explaining. Prickly pear made biological sense as it is a well-known food resource for the gopher tortoise (Ashton and Ashton 2008, Figueroa et al. 2021), with research indicating that the gopher tortoise also enhances the germination of its seeds (Richardson and Stiling 2019a).

Step 4: Locustberry (*Byrsonima lucida*)/Saw Palmetto Ratio

The final pair of fruit species that accounted for the greatest logratio variance was locustberry/saw palmetto. Locustberry is a tropical plant species that is known to be consumed by the Florida box turtle (*Terrapene carolina bauri*) (Liu et al. 2004, Platt et al. 2009). This fleshy fruit-bearing tropical shrub led the rest of the logratios when paired

with saw palmetto to explain an additional 2.81% of total variance. After this logratio, the total amount of logratio variance explained equaled 96.96% (Supp. Table II.1), at which point I stopped selecting additional logratios.

To illustrate the interrelations between the five fruit species comprising the four logratios, I created an acyclical graph where each edge connects two of the fruit species corresponding to one of the logratios I selected (Supp. Fig. II.1). In total, five fleshy-fruited species contributed to the observed shift toward frugivory – three of which were native palms and two were state threatened species in Florida (Table II.4). Subsequently, the LRA biplot illustrates the analysis of the full 16-species dataset whereas the PCA biplot depicts the ordination of the 4 logratios (Fig. II.4). While not visually obvious, the LRA biplot analyzes all 120 logratios – which can be thought of as the connections between all 16 pairs of fruit species.

In contrast, the PCA was performed only on the four logratios selected in the stepwise LRA (Fig. II.4; right panel), which shows a very similar pattern in the spread of the points as in the LRA biplot (Fig. II.4; left panel). Fall and summer samples have greater spread in them than winter and spring samples and South and West samples are more spread out than East's samples. To estimate the strength of these correlations, I calculated a Procrustes correlation of 0.976, indicating strong agreement between the two ordinations. The concordance between the LRA and PCA biplots indicate that the spatiotemporal patterns in frugivory are indeed captured by the subset of four logratios I selected out of the 120 possible. This suggests that saw palmetto, silver palm, sabal palm, prickly pear, and locustberry are important fruit resources for the gopher tortoise that drive its frugivorous dietary habit. Of the four logratios selected, the most variance-

explaining species when paired with saw palmetto are each of the following: eastern prickly pear, locustberry, sabal palm, and silver palm (Supp. Table II.2). These results suggest the most important fruit species in the diet of tortoises in the study are saw palmetto, eastern prickly pear, locustberry, sabal palm, and silver palm in that order.

2.8. GLMM for Dispersal of Endozoochorous Species

In this final analysis, I found that as frugivory increased, so did the number of endozoochorous species dispersed (Fig. II.5). The median slope value for the relationship between fruit consumption and the number of endozoochorous species dispersed was 1.34. The PD for the slope estimate was 100% and neither estimates in the lower nor upper credible intervals included zero (0.91, and 1.94 respectively), indicating it is highly probable that as frugivory increases in the gopher tortoise, so does its ecological role as a frugivore by dispersing the seeds of more species with the endozoochory syndrome.

DISCUSSION

In the present study, I quantified a temporal shift toward frugivory in a population of gopher tortoises, where fruit consumption increased with seasonal precipitation. This seasonal precipitation spurs the production of fleshy fruits in the pine rocklands of south Florida (Snyder et al. 1990, Lodge 2017), allowing this species to shift its foraging strategy. As the temporally limited fleshy fruits become increasingly available over the wet season, the gopher tortoise gradually incorporates these resources into its diet, becoming more frugivorous intra-annually.

These temporal shifts toward frugivory coincided with the calendar seasons, demonstrating that fruit consumption increased through the spring and summer, and decreased through the fall and winter. Seasonal patterns of frugivory have been documented in many other species (Koike et al. 2008, Takahashi et al. 2008), including other folivores such as the western lowland gorilla (Remis 1997). Although gopher tortoises are efficient hind-gut fermenters (Bjorndal 1987), engaging in frugivory might confer energetic and nutritional benefits that benefit life history processes such as growth and reproduction.

All three native palm species in this ecosystem facilitated the observed shift toward frugivory, along with eastern prickly pear and locustberry. Eastern prickly pear has been documented to benefit from seed dispersal through the gopher tortoise (Richardson and Stiling 2019a), while the other four species have yet been tested. However, palms are known to be widely dispersed by turtles (Falcón et al. 2020, Marques Dracxler and Kissling 2022), and saw palmetto in particular benefits from seed dispersal by the Florida box turtle in the pine rocklands of south Florida (Liu et al. 2004). If the gopher tortoise is found to enhance germination in the other four fruit species, seasonal shifts toward frugivory may translate to increased plant recruitment for these fleshy-fruit bearing plants.

On this note, I found that as frugivory increased, so did the dispersal of species with fleshy fruits, suggesting that as the gopher tortoise switches foraging strategies from folivory to frugivory, so might its functional role as a seed disperser. This alternation between folivory and frugivory can be described as a shift along the mutualism-antagonism continuum (van Leeuwen et al. 2022), by more frequently interacting with

the fruits of endozoochorous species and subsequently dispersing their seeds. With the gopher tortoise being a well-known seed disperser (MacDonald and Mushinsky 1988, Carlson et al. 2003, Birkhead et al. 2005, Figueroa et al. 2021) – known to enhance seed germination for both fleshy and non-fleshy-fruited species (Hanish 2018, Richardson and Stiling 2019a) – this study documents not only a temporal shift toward frugivory, but a shift in its functional role as a seed disperser for plants with the endozoochory syndrome (Ridley 1930, Van der Pijl 1982), although endozoochorous dispersal of plants without fleshy fruits is widespread even in the gopher tortoise (Figueroa et al. 2021, Green et al. 2021).

Considering the high degree of endemism in the pine rockland plant community (Trotta et al. 2018), and the diversity of state-threatened species dispersed by the gopher tortoise (Table II.1), the importance of seed dispersal by the gopher tortoise for plant conservation is a promising avenue for research. Conversely, the dispersal of invasive plants by the tortoises in this study raises the question of how gopher tortoises affect germination and colonization of new habitats by invasive plants, which are already widespread in south Florida (Rodgers et al. 2014).

To further unravel how endozoochorous seed dispersal varies intra-annually and how individuals of the same species may provide unique dispersal services, I encourage future studies that identify which plant species are dispersed by different individuals and how patterns of seed dispersal vary seasonally. With appropriate sampling (Jordano 2016), and using well-defined network indices (Bascompte et al. 2003, Blüthgen et al. 2006, Bascompte and Jordano 2007, Vázquez et al. 2007, Dormann et al. 2009), future research can reveal in great detail the functional differences between individuals as seed

dispersers (Bolnick et al. 2011, Zwolak 2018), and what the implications of seasonality are for plants exhibiting different dispersal syndromes.

TABLES

Endozoochorous Plant Species Recovered in Gopher Tortoise Fecal Samples		
Species	Taxonomic Family	Conservation Status
Locustberry (<i>Byrsonima lucida</i>) †	Malpighiaceae	FL Threatened
Love vine (<i>Cassytha filiformis</i>)	Lauraceae	-
Silver palm (<i>Coccothrinax argentata</i>) †	Arecaceae	FL Threatened
Rough velvetseed (<i>Guettarda scabra</i>)	Rubiaceae	-
Shrub verbena (<i>Lantana camara</i>) *	Verbenaceae	FLEPPC Cat. I Invasive
Poisonwood (<i>Metopium toxiferum</i>)	Anacardiaceae	-
West Indian Lilac (<i>Miconia bicolor</i>) †	Melastomataceae	FL Threatened
Bittermelon (<i>Momordica charantia</i>) **	Cucurbitaceae	FLEPPC Cat. II Invasive
Mouse's pineapple (<i>Morinda royoc</i>)	Rubiaceae	-
Long-stalked Stopper (<i>Mosiera longipes</i>) †	Myrtaceae	FL Threatened
Eastern prickly pear (<i>Opuntia austrina</i>)	Cactaceae	-
Walter's groundcherry (<i>Physalis walterii</i>)	Solanaceae	-
Running oak (<i>Quercus pumila</i>)	Fagaceae	-
Sabal palm (<i>Sabal palmetto</i>)	Arecaceae	-
Saw palmetto (<i>Serenoa repens</i>)	Arecaceae	-
Shiny blueberry (<i>Vaccinium myrsinites</i>)	Ericaceae	-

Table II.1. List of species whose seeds were recovered from fecal samples and classified as exhibiting the endozoochory dispersal syndrome (Ridley 1930, Van der Pijl 1982). The taxonomic families and conservation statuses of the species are included in the table. “FL Threatened” (†) means that the species is listed in the state of Florida as threatened, “FLEPPC Cat. I” (*) means the species is exotic, has increased in abundance in Florida, and demonstrated negative ecological and/or economic impacts by the Florida Exotic Pest Plant Council (FLEPPC), and “FLEPPC Cat. II” (**) represents an exotic plant species that has increased in abundance in Florida but has not yet demonstrated negative ecological or economic impacts.

Overall Season Contrasts in Frugivory				
Contrast	Lower 95% CI	Median Estimate	Upper 95% CI	PD
Spring - Winter	-0.05	-0.01	0.04	63.62%
Summer - Winter	0.07	0.13	0.19	99.99%
Fall - Winter	0.07	0.15	0.25	99.99%

Table II.2. Posterior density summary table for the effect of seasonality on overall levels of frugivory with lower 95% credible interval (CI), median estimates, upper 95% credible interval, and Probability of Direction (PD) in subsequent columns.

Within Season Shifts in Frugivory (Estimates Multiplied by 30 to Obtain Monthly Estimates)				
Season	Lower 95% CI	Median Estimate	Upper 95% CI	PD
Fall	-0.20	-0.07	0.06	86.29%
Winter	-0.11	-0.05	-0.01	99.86%
Spring	0.00	0.03	0.08	95.73%
Summer	0.02	0.08	0.14	99.71%

Table II.3. Posterior density summary table for the effect of seasonality on within-season frugivory with lower 95% credible interval (CI), median estimates, upper 95% credible interval, and Probability of Direction (PD) in subsequent columns.

Logratio Analysis Summary Table for all Fruit Species				
Fruit Species	Family	Inertia	Dim. 1	Dim. 2
Saw palmetto (<i>Serenoa repens</i>)	Arecaceae	0.711602	-1.49576	0.085342
Sabal palm (<i>Sabal palmetto</i>)	Arecaceae	0.116705	0.489575	-3.376349
Eastern prickly pear (<i>Opuntia austrina</i>)	Cactaceae	0.091348	0.772435	0.853837
Locustberry (<i>Byrsonima lucida</i>)†	Malpighiaceae	0.068603	0.802306	0.647139
Silver palm (<i>Coccothrinax argentata</i>)†	Arecaceae	0.063593	0.681746	0.298484
Long-stalked stopper (<i>Mosiera longipes</i>)†	Myrtaceae	0.057499	0.647672	0.27944
Shrub verbena (<i>Lantana camara</i>)*	Verbenaceae	0.034346	0.764271	0.373817
Rough velvetseed (<i>Guettarda scabra</i>)	Rubiaceae	0.023708	0.609351	0.325613
Running oak (<i>Quercus pumila</i>)	Fagaceae	0.0154	0.693592	0.325157
Bittermelon (<i>Momordica charantia</i>)**	Cucurbitaceae	0.015171	0.693848	0.297156
Love vine (<i>Cassytha filiformis</i>)	Lauraceae	0.011483	0.649683	0.268419
Shiny blueberry (<i>Vaccinium myrsinites</i>)	Ericaceae	0.011414	0.665185	0.256794
Poisonwood (<i>Metopium toxiferum</i>)	Anacardiaceae	0.010983	0.656048	0.242559
West Indian lilac (<i>Miconia bicolor</i>)†	Melastomataceae	0.010652	0.590305	0.307628
Mouse's pineapple (<i>Morinda royoc</i>)	Rubiaceae	0.010143	0.642664	0.272178
Walter's groundcherry (<i>Physalis walterii</i>)	Solanaceae	0.009935	0.628594	0.290966

Table II.4. Summary table of the logratio analysis for all 16 fruit species, ordered from most to least inertia captured by each. Taxonomic families are included, and conservation status is symbolized as in Table II.1. Dim. 1 and Dim. 2 are the principal coordinates for each axis.

FIGURES

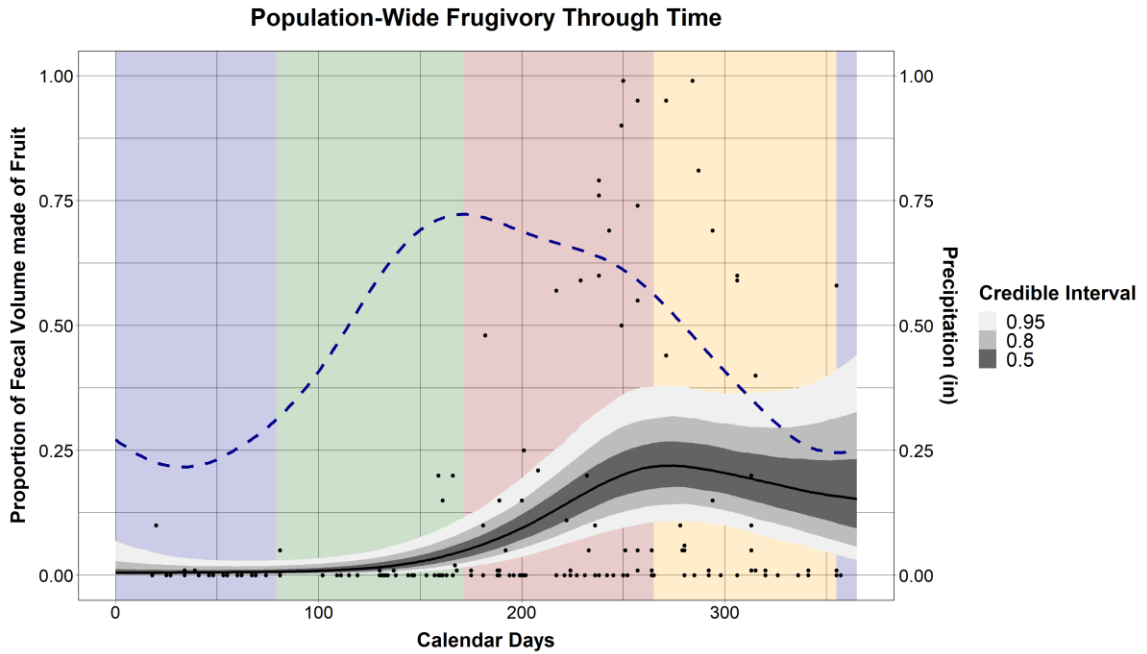


Figure II.1. Spline plot generated by Generalized Additive Mixed Models (GAMM), which illustrates the temporal increase and decrease in precipitation (blue dashed line) and frugivory (gray spline with credible intervals). Black points represent each fecal sample and the colored rectangles in the background represent the calendar seasons. The horizontal axis is the number of calendar days elapsed in the year, the left vertical axis is the proportion of fecal volume comprised of fruit, and the right vertical axis is the average daily precipitation. Winter is blue, spring is green, summer is red, and fall is orange. The progressively lighter intervals surrounding each curve represent the Bayesian 50%, 80%, and 95% credible intervals.

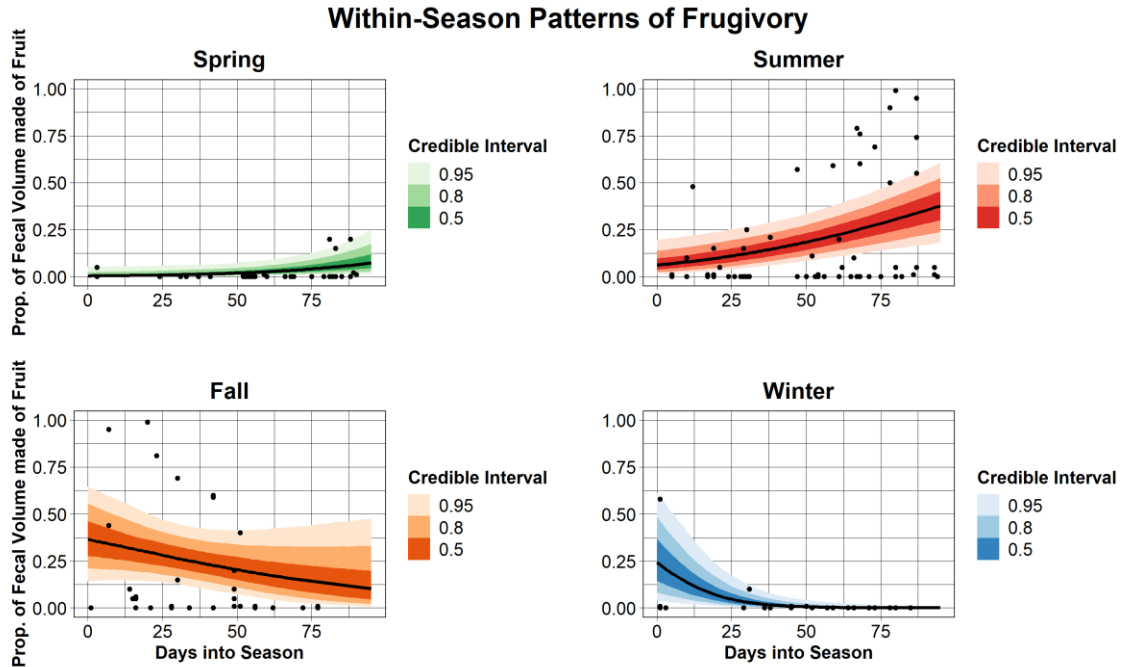


Figure II.2. Regression plots generated by the Generalized Linear Mixed Model (GLMM), which depicts the within-season trends in frugivory. Black points represent fecal samples collected in the season that the panel corresponds to, with the season labeled above it. The horizontal axis is the number of days in each season and the vertical axis is the proportion of fecal volume comprised of fruit. The progressively lighter intervals surrounding the curves in each panel represent the Bayesian 50%, 80%, and 95% credible intervals.

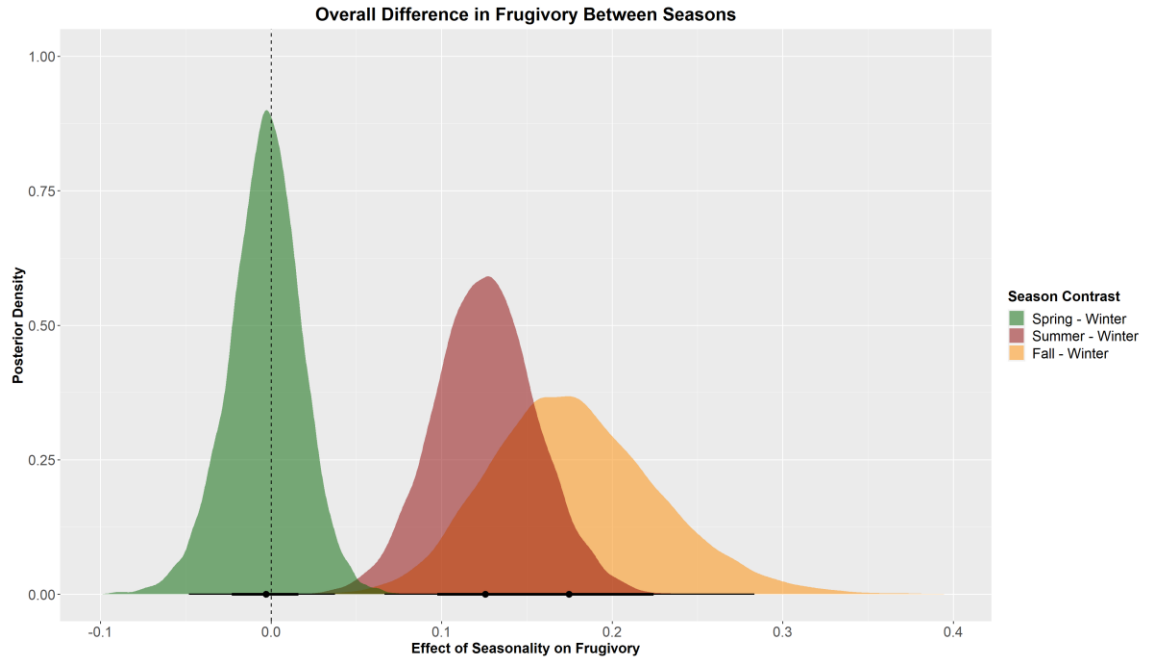


Figure II.3. Density plot from the GLMM estimates showing the effect of seasonality on overall levels of frugivory. The values along the x-axis indicate the overall difference in frugivory between the season of interest and winter. The spring-winter contrast is in green, summer-winter contrast is in red, and fall-winter contrast is in orange.

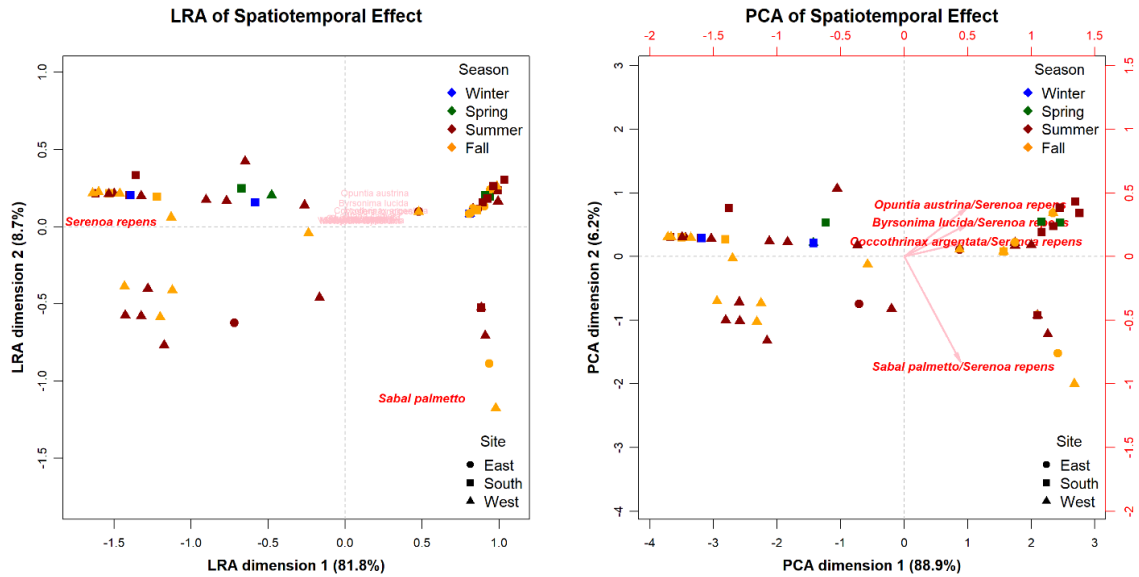


Figure II.4. Left panel: Logratio analysis (LRA) contribution biplot of the frugivory dataset. The fleshy fruits that contribute more than average to the total variance are more outlying and shown in large red text while all others are closer to the center of the biplot and shown in smaller pink font. Blue, green, red, and orange show the influence of fleshy fruits on the population's frugivory during the winter, spring, summer, fall seasons, respectively. On the other hand, circles represent the East site, squares represent South, and triangles represent West. Right panel: PCA contribution biplot of the four logratios identified in the stepwise variable selection process that explain 96.96% of the total logratio variance in the frugivory dataset (the two-dimensional PCA explains 95.1% of the total 96.96%, according to the percentages captured in both axes).

Effect of Frugivory on Dispersal of Endozoochorous Species

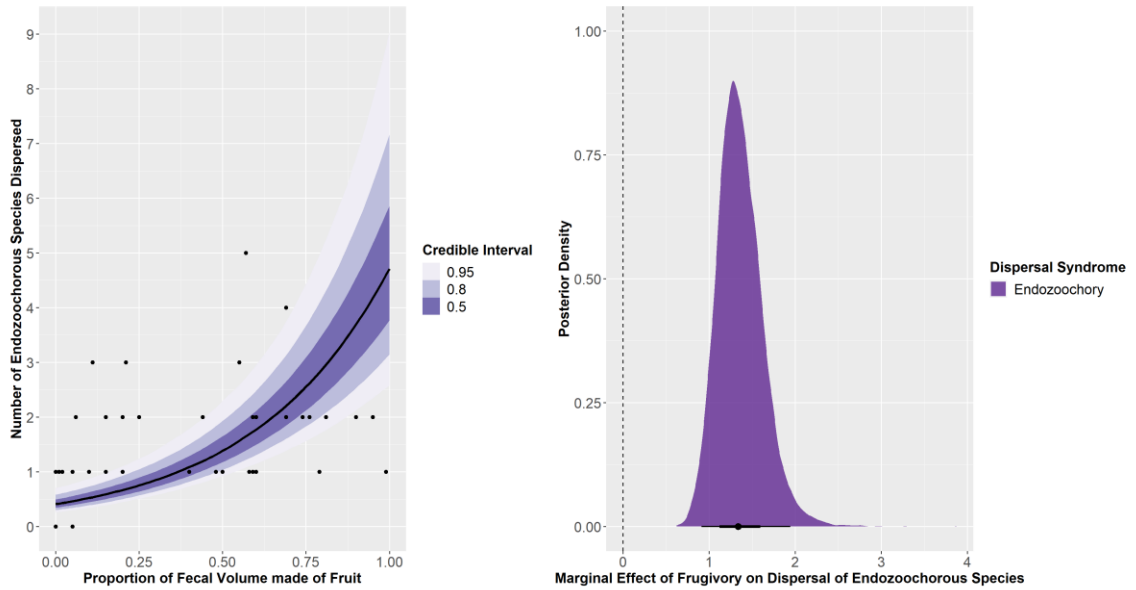


Figure II.5. Left panel: Regression plot generated by the Generalized Linear Mixed Model (GLMM) which depicts the effect of frugivory on seed dispersal for species with the endozoochory syndrome (purple). Black points represent the number of species with the endozoochory syndrome dispersed for a given degree of frugivory. The horizontal axis is the proportion of fruit in the fecal sample, and the vertical axis is the number of species dispersed. The progressively lighter intervals surrounding each curve represent the Bayesian 50%, 80%, and 95% credible intervals. Right panel: Density plot illustrating the posterior slope estimates for species with the endozoochory syndrome (purple).

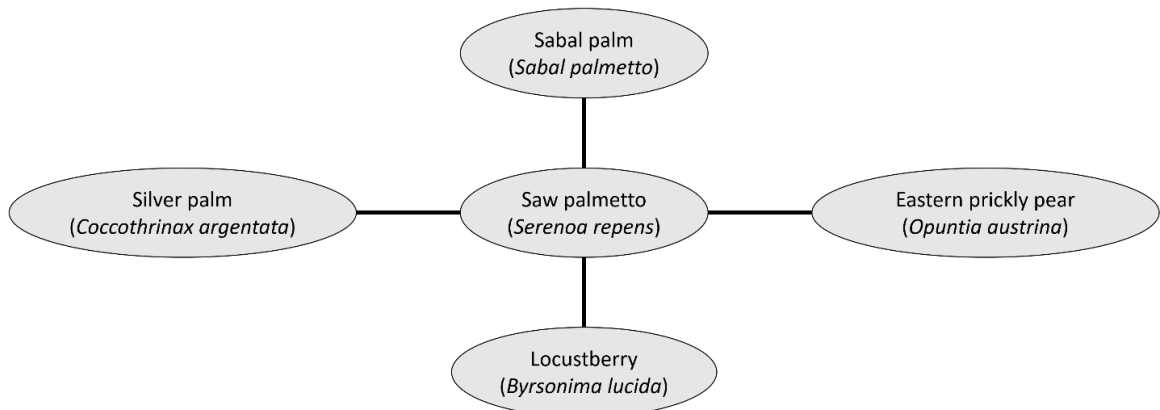
SUPPLEMENTARY TABLES AND FIGURES

Logratio Variance Explained at each Step by Pairs of Fruit Species			
Step	Logratio Species Pair	Additional Variance Explained	Cumulative Variance Explained
1	Cocarg/Serrep	80.97%	80.97%
2	Sabpal/Serrep	8.57%	89.54%
3	Opuaus/Serrep	4.61%	94.15%
4	Byrluc/Serrep	2.81%	96.96%

Supplementary Table II.1. Summary table for each step in the logratio selection process depicting the species pairs comprising each logratio with the additional and cumulative variance explained in subsequent columns. Species names in each logratio are written as a concatenation of the first three characters in the genus and species, brought together by a forward slash in between (e.g., Cocarg/Serrep is *Coccothrinax argentata* with *Serenoa repens*).

Principal Component Analysis Summary Table for all Fruit Species			
Logratio Species Pair	Inertia	Dim. 1	Dim. 2
Opuaus/Serrep	1.528439	1.041669	-0.808118
Byrluc/Serrep	1.515354	1.047124	-0.528239
Sabpal/Serrep	1.34722	0.930279	1.736873
Cocarg/Serrep	1.23717	0.976237	-0.22623

Supplementary Table II.2. Summary table for the PCA listing the logratios in descending order from most to least inertia captured. Additional columns include the coordinates for each axis.



Supplementary Figure II.1. Acyclic graph of the four fleshy fruit species in the frugivory dataset that explain the majority of logratio variance. Each edge links the pair of fleshy fruits that define one of the four logratios.

LITERATURE CITED

- Abrahms, B., E. O. Aikens, J. B. Armstrong, W. W. Deacy, M. J. Kauffman, and J. A. Merkle. 2021. Emerging Perspectives on Resource Tracking and Animal Movement Ecology. *Trends in Ecology & Evolution* 36:308–320.
- Ashton, R. E., and P. S. Ashton. 2008. The Natural History and Management of the Gopher Tortoise. *Gopherus polyphemus*:65–93.
- Auffenberg, W., and R. Franz. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). *North American Tortoises: Conservation Ecology*:95–126.
- Bascompte, J., and P. Jordano. 2007. Plant-animal mutualistic networks: The architecture of biodiversity. *Annual Review of Ecology Evolution and Systematics* 38:567–593.
- Bascompte, J., P. Jordano, C. J. Melián, and J. M. Olesen. 2003. The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences* 100:9383.
- Birkhead, R. D., C. Guyer, S. M. Hermann, and W. K. Michener. 2005. Patterns of folivory and seed ingestion by gopher tortoises (*Gopherus polyphemus*) in a southeastern pine savanna. *American Midland Naturalist* 154:143–151.
- Bjorndal, K. A. 1987. Digestive Efficiency in a Temperate Herbivorous Reptile, *Gopherus polyphemus*. *Copeia* 1987:714–720.
- Blüthgen, N., F. Menzel, and N. Blüthgen. 2006. Measuring specialization in species interaction networks. *BMC Ecology* 6:9.
- Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution* 26:183–192.
- Bradley, K. A., and G. D. Gann. 2005. *Natural Forest Community Delineation Methods*. The Institute for Regional Conservation.
- Bronstein, J. L. 2015. *Mutualism*. Oxford University Press.
- Bürkner, P.-C. 2017. brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software* 80:1–28.
- Bürkner, P.-C. 2018. Advanced Bayesian Multilevel Modeling with the R Package brms. *R Journal* 10:395–411.

- Bürkner, P.-C. 2021. Bayesian Item Response Modeling in R with brms and Stan. *Journal of Statistical Software* 100:1–54.
- Bury, R. B., and D. J. Germano. 1994. *Biology of North American tortoises*. Report, Washington, D.C.
- Carlson, J. E., E. S. Menges, and P. L. Marks. 2003. Seed dispersal by *Gopherus polyphemus* at Archbold Biological Station, Florida. *Florida Scientist* 66:147–154.
- Carr, A. F. 1940. Contribution to the herpetology of Florida.
- Chase, J. M., and M. A. Leibold. 2009. Ecological niches. Page *Ecological Niches*. University of Chicago Press.
- Diamond, J. M., and J. T. Heinen. 2016. Conserving rare plants in locally-protected urban forest fragments: A case study from Miami-Dade County, Florida. *Urban Forestry & Urban Greening* 20:1–11.
- Diemer, J. E. 1986. The Ecology and Management of the Gopher Tortoise in the Southeastern United States. *Herpetologica* 42:125–133.
- Dormann, C. F., J. Fründ, N. Blüthgen, and B. Gruber. 2009. Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Ecology Journal* 2.
- Edwards, T., A. Karl, M. Vaughn, P. Rosen, C. Meléndez Torres, and R. Murphy. 2016. The desert tortoise trichotomy: Mexico hosts a third, new sister-species of tortoise in the *Gopherus morafkai*–*G. agassizii* group. *ZooKeys* 562:131–158.
- Elton, C. S. 2001. *Animal Ecology*. Page (M. A. Leibold and T. J. Wootton, Eds.). University of Chicago Press, Chicago, IL.
- Enge, K. M., M. S. Robson, and K. L. Krysko. 2004. Reptile surveys of pine rockland habitat in six Miami-Dade County parks. *Florida Scientist* 67:194–204.
- Falcón, W., D. Moll, and D. M. Hansen. 2020. Frugivory and seed dispersal by chelonians: a review and synthesis. *Biol Rev Camb Philos Soc*.
- Figueroa, A., J. T. Heinen, F. N. Ridgley, S. M. Whitfield, and H. Liu. 2023. Management of a Globally Imperiled and Fire-Dependent Ecosystem in the Urban Matrix of Miami–Dade County, Florida: A Case Study of the Richmond Tract Pine Rocklands. *Diversity* 15:426.
- Figueroa, A., J. Lange, and S. M. Whitfield. 2021. Seed Consumption by Gopher Tortoises (*Gopherus polyphemus*) in the Globally Imperiled Pine Rockland Ecosystem of Southern Florida, USA. *Chelonian Conservation and Biology* 20:27–34, 8.

- Flora of North America Editorial Committee, eds. 1993+. 2023. Flora of North America North of Mexico [Online]. New York and Oxford.
- Florida Natural Areas Inventory. 2010. Guide to the Natural Communities of Florida.
- Gann, G. D., C. G. Stocking, and Collaborators. 2001. Floristic Inventory of South Florida Database Online. The Institute for Regional Conservation. Delray Beach, Florida.
- Gann, G. D., S. W. Woodmansee, and K. A. Bradley. 2002. Rare plants of south Florida: their history, conservation and restoration. Institute for Regional Conservation.
- Gerardo Herrera M., L., C. Korine, T. H. Fleming, and Z. Arad. 2008. Dietary Implications of Intrapopulation Variation in Nitrogen Isotope Composition of an Old World Fruit Bat. *Journal of Mammalogy* 89:1184–1190.
- Graeve, M., and M. J. Greenacre. 2020. The selection and analysis of fatty acid ratios: A new approach for the univariate and multivariate analysis of fatty acid trophic markers in marine pelagic organisms. *Limnology and Oceanography: Methods* 18:196–210.
- Grant, C. 1960. Differentiation of the southwestern tortoises (genus *Gopherus*) with notes on their habits. *Transactions of the San Diego Society of Natural History* 12:441–448.
- Green, A. J., C. Baltzinger, and Á. Lovas-Kiss. 2021. Plant dispersal syndromes are unreliable, especially for predicting zoochory and long-distance dispersal. *Oikos*.
- Greenacre, M. 2018. *Compositional Data Analysis in Practice*. Chapman and Hall/CRC.
- Greenacre, M. 2019. Variable Selection in Compositional Data Analysis Using Pairwise Logratios. *Mathematical Geosciences* 51:649–682.
- Greenacre, M. 2021. Compositional Data Analysis. *Annual Review of Statistics and Its Application* 8:271–299.
- Guyer, C., V. M. Johnson, and S. M. Hermann. 2012. Effects of Population Density On Patterns of Movement and Behavior of Gopher Tortoises (*Gopherus polyphemus*). *Herpetological Monographs* 26:122–134.
- Hanish, C. J. 2018. Seed Dispersal of the Cocoplum (*Chrysobalanus icaco*) by Gopher Tortoises (*Gopherus polyphemus*) in Southeastern Florida. Florida Atlantic University.
- Hoffmeister, J. E., K. W. Stockman, and H. G. Multer. 1967. Miami Limestone of Florida and its recent Bahamian counterpart. *Geological Society of America Bulletin* 78:175–190.

- Jordano, P. 2016. Sampling networks of ecological interactions. *Functional Ecology* 30:1883–1893.
- Klare, U., J. F. Kamler, and D. W. MacDonald. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review* 41:294–312.
- Koike, S., S. Kasai, K. Yamazaki, and K. Furubayashi. 2008. Fruit phenology of *Prunus jamasakura* and the feeding habit of the Asiatic black bear as a seed disperser. *Ecological Research* 23:385–392.
- Kubinec, R. 2022. Ordered Beta Regression: A Parsimonious, Well-Fitting Model for Continuous Data with Lower and Upper Bounds. *Political Analysis*:1–18.
- Kushlan, J. A., and F. J. Mazzotti. 1984. Environmental Effects on a Coastal Population of Gopher Tortoises. *Journal of Herpetology* 18:231–239.
- van Leeuwen, C. H. A., N. Villar, I. Mendoza Sagera, A. J. Green, E. S. Bakker, M. B. Soons, M. Galetti, P. A. Jansen, B. A. Nolet, and L. Santamaría. 2022. A seed dispersal effectiveness framework across the mutualism–antagonism continuum. *Oikos*:e09254.
- Lips, K. R. 1991. Vertebrates Associated with Tortoise (*Gopherus polyphemus*) Burrows in 4 Habitats in South-Central Florida. *Journal of Herpetology* 25:477–481.
- Liu, H., S. G. Platt, and C. K. Borg. 2004. Seed dispersal by the Florida box turtle (*Terrapene carolina bauri*) in pine rockland forests of the lower Florida Keys, United States. *Oecologia* 138:539–546.
- Lodge, T. E. 2017. *The Everglades Handbook: Understanding the Ecosystem (Fourth Edition)*. Everglades Handbook: Understanding the Ecosystem, 4th Edition.
- MacDonald, L. A., and H. R. Mushinsky. 1988. Foraging Ecology of the Gopher Tortoise, *Gopherus polyphemus*, in a Sandhill Habitat. *Herpetologica* 44:345–353.
- Makowski, D., M. S. Ben-Shachar, S. H. A. Chen, and D. Lüdtke. 2019. Indices of Effect Existence and Significance in the Bayesian Framework. *Frontiers in Psychology* 10:2767.
- Marques Dracxler, C., and W. D. Kissling. 2022. The mutualism–antagonism continuum in Neotropical palm–frugivore interactions: from interaction outcomes to ecosystem dynamics. *Biological Reviews* 97:527–553.
- McRae, W. A., J. L. Landers, and J. A. Garner. 1981. Movement Patterns and Home Range of the Gopher Tortoise. *The American Midland Naturalist* 106:165–179.
- Monroe, M. B. 1943. Pioneer Women of Dade County. *Tequesta* 1:54–55.

- Mushinsky, H. R., T. A. Stilson, and E. D. McCoy. 2003. Diet and dietary preference of the juvenile gopher tortoise (*Gopherus polyphemus*). *Herpetologica* 59:475–483.
- Pavelka, M. S. M., and K. H. Knopff. 2004. Diet and activity in black howler monkeys (*Alouatta pigra*) in southern Belize: does degree of frugivory influence activity level? *Primates* 45:105–111.
- Pedersen, E. J., D. L. Miller, G. L. Simpson, and N. Ross. 2019. Hierarchical generalized additive models in ecology: an introduction with mgcv. *PeerJ* 7:e6876.
- Platt, S. G., C. Hall, H. Liu, and C. K. Borg. 2009. Wet-season Food Habits and Intersexual Dietary Overlap of Florida Box Turtles (*Terrapene carolina bauri*) on National Key Deer Wildlife Refuge, Florida. *Southeastern Naturalist* 8:335–346.
- Possley, J., J. Duncan, J. Gil, and C. Grossenbacher. 2020. Too Precious To Lose: Managing and Protecting the Richmond Pine Rockland Tract (Richmond) in Miami Dade County, South Florida. *Cities and the Environment* 13.
- Possley, J., J. Duncan, J. Klein, and J. Maguire. 2018. Miami-Dade County's Management Plan for the Richmond Pine Rocklands, 2nd ed. Prepared by Fairchild Tropical Botanic Garden for Miami-Dade County, Department of Parks, Recreation and Open Spaces and Zoo Miami 2:136.
- Possley, J., S. W. Woodmansee, and J. Maschinski. 2008. Patterns of Plant Composition in Fragments of Globally Imperiled Pine Rockland Forest: Effects of Soil Type, Recent Fire Frequency, and Fragment Size. *Natural Areas Journal* 28:379–394.
- R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Remis, M. J. 1997. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: Use of variable resources. *American Journal of Primatology* 43:87–109.
- Richardson, J. C., and P. Stiling. 2019a. Gopher Tortoise (*Gopherus polyphemus*) Gut Passage Can Alter Seed Germinability. *The American Midland Naturalist* 182:181–190.
- Richardson, J. C., and P. Stiling. 2019b. Gopher tortoise herbivory increases plant species richness and diversity. *Plant Ecology* 220:383–391.
- Ridley, H. N. 1930. *The dispersal of plants throughout the world*. L. Reeve & Company, Limited.
- Robira, B., S. Benhamou, T. N. Fuh, and S. Masi. 2023. Do Seasonal Frugivory and Cognition Shape Foraging Movements in Wild Western Gorillas? Pages 151–170 in R. Reyna-Hurtado, C. A. Chapman, and M. Melletti, editors. *Movement*

- Ecology of Afrotropical Forest Mammals. Springer International Publishing, Cham.
- Rodgers, L., T. Pernas, and S. D. Hill. 2014. Mapping Invasive Plant Distributions in the Florida Everglades Using the Digital Aerial Sketch Mapping Technique. *Invasive Plant Science and Management* 7:360–374.
- Schupp, E. W. 1993. Quantity, Quality and the Effectiveness of Seed Dispersal by Animals. *Vegetatio* 108:15–29.
- Schupp, E. W., P. Jordano, and J. M. Gómez. 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist* 188:333–353.
- Simpson, C. T. 1920. In lower Florida wilds:174–184.
- Snyder, J. R., A. Herndon, and W. B. Robertson Jr. 1990. South Florida Rockland. *Ecosystems of Florida*:230–277.
- Takahashi, K., T. Shiota, H. Tamatani, M. Koyama, and I. Washitani. 2008. Seasonal variation in fleshy fruit use and seed dispersal by the Japanese black bear (*Ursus thibetanus japonicus*). *Ecological Research* 23:471–478.
- Traveset, A., R. Heleno, and M. Nogales. 2014. The Ecology of Seed Dispersal. *Seeds: The Ecology of Regeneration in Plant Communities*, 3rd Edition:62–93.
- Trotta, L. B., B. Baiser, J. Possley, D. J. Li, J. Lange, S. Martin, and E. B. Sessa. 2018. Community phylogeny of the globally critically imperiled pine rockland ecosystem. *American Journal of Botany* 105:1735–1747.
- USFWS. 1999. Pine Rocklands Management Plan.
- Van der Pijl, L. 1982. Principles of dispersal in higher plants. Springer.
- Vázquez, D. P., C. J. Melián, N. M. Williams, N. Blüthgen, B. R. Krasnov, and R. Poulin. 2007. Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116:1120–1127.
- Waddle, J. H., F. J. Mazzotti, and K. G. Rice. 2006. Changes in Abundance of Gopher Tortoise Burrows at Cape Sable, Florida. *Southeastern Naturalist* 5:277–284, 8.
- Whitfield, S. M., F. N. Ridgley, D. Valle, and N. Atteberry. 2018. Seroprevalence of *Mycoplasma agassizii* and *Mycoplasma testudineum* in Wild and Waif Gopher Tortoises (*Gopherus polyphemus*) in Miami-Dade County, Florida, USA. *Herpetological Review* 49:47–49.
- Whitfield, S. M., D. Valle, A. Figueroa, B. Chin, H. Bravo-Gallegos, and F. Leone. 2022. Burrow Characteristics and Habitat Associations of Gopher Tortoises in Urban

Pine Rockland Reserves (Miami, Florida, USA). *Ichthyology & Herpetology* 110:22–32.

Wood, S. N. 2006. *Generalized additive models: an introduction with R*. Chapman and Hall/CRC.

World Wildlife Fund. 2014. *South Florida rocklands*.

Wunderlin, R. P., B. F. Hansen, A. R. Franck, and F. B. Essig. 2016. *Atlas of Florida vascular plants*. Atlas of Florida vascular plants.

Zwolak, R. 2018. How intraspecific variation in seed-dispersing animals matters for plants. *Biological Reviews* 93:897–913.

CHAPTER III. ANALYSIS OF AN INTRASPECIFIC SEED DISPERSER
NETWORK: IMPORTANCE OF DISPERSER MORPHOLOGY,
SEASONALITY, AND DISPERSAL SYNDROMES IN MEDIATING
INTERACTIONS

INTRODUCTION

Seed dispersal is a crucial ecological process, involving diverse flora and fauna from all over the world (Levey et al. 2002, Dennis 2007). Decades of study have revealed the importance of seed dispersal for the maintenance of biodiversity and the provisioning of ecosystem services (Howe and Smallwood 1982, Traveset et al. 2014). Specifically, animal-mediated seed dispersal is a critical dispersal mechanism, directing seeds to favorable microsites and enhancing germination rates through digestive processes (Howe 1986, Traveset 1998, Wenny 2001). Tremendous effort has been put into studying the effectiveness of species as seed dispersers (Schupp 1993, Jordano and Schupp 2000, Schupp et al. 2010), both in their movement of seeds and in their influence on germination (Nathan and Muller-Landau 2000, Nathan et al. 2000, Traveset et al. 2007), but most studies have been conducted at the species rather than individual level, potentially masking important variation among conspecifics in their functional roles as seed dispersers (Zwolak 2018).

Traits that vary intra-specifically, such as body size, gape size, and even personality may influence the functional role of seed dispersers (Galetti et al. 2013, Zwolak 2018, Zwolak and Sih 2020). Even social status has been demonstrated to influence dispersal services provided by conspecifics (Bartel and Orrock 2022). Furthermore, individuals of the same species have been widely documented to specialize

on resources not frequently used by the rest of the population (Bolnick et al. 2007, Coblenz et al. 2017, Balme et al. 2020). This phenomenon is known as individual diet specialization and is caused by diverse ecological processes, such as the availability of resources (Araújo et al. 2011). Individual diet specialization has been documented in frugivorous species where seasonal differences in fruit availability results in greater diet specialization when fruits are more widely available (Gerardo Herrera M. et al. 2008). Therefore, temporal differences in frugivory may result in different seed dispersal interactions, shaping the diversity of fruits and seeds that animals ingest and disperse (Fuh et al. 2022).

A comprehensive way to gauge how species – or individuals – differ in their roles as seed dispersers is through the application of network theory (Bascompte 2009, Donatti et al. 2011, Bascompte and Jordano 2014). Ecological networks form the wireframe of biodiversity (Bascompte and Jordano 2007, Jordano 2016a), and provide a foundation for unravelling how species interact with one another. Networks provide insight into how connected seed dispersers are to the plant community as well as how resilient the plant community is to the extinction of one or more partner seed dispersers (Bascompte et al. 2003, Blüthgen et al. 2006, 2008, Dormann et al. 2009, Vázquez et al. 2009). By applying a network approach to analyze intra-specific seed dispersal interactions, one can quantify both network-level measures of – for example – modularity, nestedness and connectance, and the individual-level role of seed dispersers as specialists or generalists in the network (Blüthgen et al. 2006, 2008, Almeida-Neto et al. 2008). Network theory allows us to test what individual-specific traits influence the degree of specialization of

individuals as well as other individual-level network indices (Vizentin-Bugoni et al. 2021).

In this study, I construct and analyze an intraspecific seed disperser network and discuss the role of conspecific individuals in the network's structure, as well as the role of seasonality in shaping seed dispersal interactions. I aim to address the following questions: 1) What are emergent patterns in intraspecific seed disperser networks and how do they compare with null predictions? 2) Which disperser traits shape interaction specialization? 3) How dissimilar are the wet and dry season subnetworks, and how much is attributed to species turnover versus rewiring? and 4) Do node-level indices of network specialization differ between the dry and wet seasons?

METHODS

3.1. Site Description

This study took place in the globally imperiled pine rockland ecosystem (World Wildlife Fund 2014), which is the most plant diverse ecological community in southern Florida, USA (Trotta et al. 2018). Specifically, this project was conducted in the Richmond Tract pine rocklands of Miami-Dade County, Florida (Possley et al. 2018, Figueroa et al. 2023), which harbors a diversity of native and endemic plants (Possley et al. 2008, Diamond and Heinen 2016). The pine rockland flora and fauna represent the confluence of temperate and neotropical species at the southern and northern extents of their ranges, respectively (Snyder et al. 1990, Trotta et al. 2018). This ecosystem is characterized by a scant canopy of endemic south Florida slash pine (*Pinus elliotti* var.

densa), a shrubby layer of fleshy fruit-producing plants, and a groundcover layer littered with many endemic species found nowhere else (Lodge 2017).

In south Florida, seasonal fluctuations in temperature are less pronounced than that of rainfall. Here, summer and fall are considered the wet season (May/June to October/November) and winter and spring the dry season (November/December to April/May) (Lodge 2017). As a result of these pronounced differences in precipitation, the phenology of many plants in this community coincides with these seasonal changes in rainfall (Flora of North America Editorial Committee, eds. 1993+ 2023), making this system a great model to investigate the role of seasonality on seed dispersal dynamics.

3.2. Study Species

The focal seed disperser of this study is the gopher tortoise (*Gopherus polyphemus*). The gopher tortoise is the only native tortoise found east of the Mississippi and Tombigbee rivers (Auffenberg and Franz 1978, 1982), and has been documented as southeast as the Miami pine rocklands by early homesteaders (Simpson 1920, Monroe 1943). As its name suggests, the gopher tortoise is recognized for its burrowing behavior that modifies surrounding habitat, supporting the persistence of more than 350 commensal species (Diemer 1986, Lips 1991). Even at the southeastern extent of this species' range, in the pine rocklands, it supports a host of commensals (Melanson 2021).

In addition to its burrowing behavior, the gopher tortoise profoundly modifies its habitat through its key role as an herbivore (Richardson and Stiling 2019b), and prolific seed disperser (Carlson et al. 2003, Mushinsky et al. 2003, Birkhead et al. 2005, Hanish 2018, Richardson and Stiling 2019a, Figueroa et al. 2021). With its generalist

herbivorous and frugivorous diet, foraging on over 1000 plant species across its range (Ashton and Ashton 2008), the gopher tortoise is a model species to investigate seed dispersal interactions with the hyper diverse pine rockland flora (Trotta et al. 2018).

3.3. Study Design

Scat Collection and Dissection

To sample the network as completely as possible (*sensu* Jordano 2016b), the tortoises in this study were tracked twice weekly via radio telemetry for 1.5 years – from May 11, 2021, to November 22, 2022 – and seeds of all plant species recovered from fecal samples, were included in the network. Over the course of the study period, uniquely marked individuals were handled as part of ongoing research activities and oftentimes produced fecal samples. These samples were collected and labeled with the individual's ID, the date collected, and the GPS location where the tortoise was during scat collection. The tortoises in the study were concentrated in three spatial aggregations I refer to as the East, South, and West sites (Fig. I.1). These aggregations are likely caused by the social behavior of the gopher tortoise (Guyer et al. 2012), as well as the geology of the pine rocklands which limits the availability of sandy soil for burrowing (Hoffmeister et al. 1967, Whitfield et al. 2022).

The three tortoise sites represent a gradient from best to worst quality habitat as determined by fire frequency and invasive species cover (Snyder 1991, Possley et al. 2018), with the West site being the best and the East site the worst. While formal floristic surveys were not performed, there was a striking and obvious monoculture of invasive plant cover – particularly of Burma reed (*Neyraudia reynaudiana*) – in the East tortoise

aggregation than in either the South or West sites. Clonally reproducing rhizomatous grasses are known to spread prolifically and reduce native plant diversity (Klein and Smith 2021), which could subsequently affect the fruits and seeds available for consumption by the tortoises in the East site compared to the South or West. As a result, I expected that individuals from the East site may form a distinct module in the network.

Once samples were collected, they were dissected with forceps and all identifiable seeds were extracted from the feces. Seeds were identified to the lowest taxonomic unit with consultation from expert botanists, dichotomous keys, and online references (Gann et al. 2001, 2002, Wunderlin et al. 2016), and were subsequently counted. All seeds recovered from fecal samples were recorded as either having the classical “endozoochory” (i.e., fleshy fruit) syndrome (Ridley 1930, Van der Pijl 1982), or having some other syndrome which I labeled as “other,” since the focus here is to assess the influence of fleshy fruits on seasonal changes in network structure.

Measuring Individual-Level Traits

To consider individual-level traits and their influence on network properties, I measured the straight-line carapace length, carapace width, and gape size for each tortoise at least once. Given the short duration of the study compared to the life history stages of the gopher tortoise (Ashton and Ashton 2008, Rostal et al. 2014), I do not believe changes in carapace/gape size in this time frame would affect the results. When possible, I recorded multiple body mass measurements from individuals to account for body condition at the time of sampling and averaged these values for each tortoise.

3.4. Statistical Analysis

All statistical analyses were carried out in R version 3.3.0 using various packages that are explicitly stated in the following subsections (R Core Team 2022).

3.4.1. Constructing the Full Intraspecific Seed Disperser Network and Seasonal Subnetworks

To assess the role conspecifics play in seed dispersal networks, I used the bipartite package in R to construct the network (Dormann et al. 2008). I weighed interactions based on the proportion of an individual's samples that included a particular species throughout the whole study for the full network and within each season for the seasonal subnetworks. For this, I only included interactions with plants identified to the species level. Following the criteria of Vizentin-Bugoni et al. (2019), I excluded all individuals for which I had less than four samples in the whole study for the full network and within each season for the seasonal subnetworks to avoid overestimating interaction intensity. For the seasonal subnetworks, any tortoises that were present in one subnetwork but not another were omitted to avoid overrepresenting the influence of some individuals over others in the network's structure.

The full study-wide network was then constructed which included all individuals from all sites that provided at least four samples. Subsequently, the seasonal subnetworks were constructed where only samples collected in the wet (June through November) or dry (December through May) seasons were included in the same network. This separation allowed us to analyze the effect seasonality on seed dispersal interactions.

3.4.2. Calculating Network-Level Indices

To understand the structure of intraspecific seed disperser networks, I calculated complementary specialization ($H2'$), weighted nestedness (wNODF), weighted modularity (Q_w), linkage density, and interaction evenness using the `networklevel()` function in the `bipartite` package (Blüthgen et al. 2006, 2008, Dormann et al. 2008). These network metrics provide insights into network-wide specialization, as well as the redundancy, compartmentalization, density, and evenness of interactions, respectively (Blüthgen et al. 2006, 2008, Bascompte and Jordano 2007, 2014, Bascompte 2009). To test for statistical significance of each observed network index, I generated 1000 null networks based on the full network as well as both seasonal subnetworks using the `vaznull` method in the `bipartite` package (Dormann et al. 2009, Vázquez et al. 2009).

The `vaznull` approach produces null model networks with the same connectance as the reference network as its main constraint, which allows users to compare observed network-level indices from the reference networks to the expectation from the null network permutations. I calculated p-values of the observed network-level indices when compared to the null networks using Standardized Effect Sizes (SES) calculated by following Gotelli and McCabe (2002). SES values are calculated by subtracting the null expectation for the index of interest from the observed value in the reference network and subsequently dividing by the standard deviation of values from the null network permutations.

To quantify the number and identify of modules in the full network, I used the `metaComputeModules()` and `plotModuleWeb()` functions from the `bipartite` package (Dormann et al. 2008). These functions allowed us to identify modules in the full

network, illustrating which plant species and individual tortoises interact more with one another they do with other potential partners in the network (Donatti et al. 2011).

3.4.3. Calculating Node-Level Indices

Focusing on the role of individual tortoises and fleshy-fruited species in the network, I then calculated node-level network indices using the `specieslevel()` function from the `bipartite` package (Dormann et al. 2008), which is intended to calculate node-level metrics as I do here. I calculated partner diversity, normalized degree, and interaction specialization (i.e., Blüthgen's d') (Blüthgen et al. 2006, Dormann et al. 2008). Partner diversity is the diversity of plant species that an individual tortoise is dispersing or the diversity of tortoises in the population that dispersed the seeds of a particular plant species – which is calculated using the Shannon diversity index. Normalized degree is the proportion of all possible interactions that the individual tortoise/plant species participates in within the network, and Blüthgen's d' is an index used to quantify the degree of specialization or generality of an individual tortoise/plant species in the network by preferentially interacting with a subset of potential partners. As in the case for the network-level indices, I generated null networks to quantify the statistical significance of the findings. However, here I used the Holm-Bonferroni multiple comparisons correction to avoid making a Type I or Type II error in the interpretation of the results since each network resulted in multiple node-level calculations (Armstrong 2014).

3.4.4. Modeling Effect of Morphological Traits on Network Specialization

After calculating the node-level network indices for the full network and testing for significance, I used the Bayesian brms R package (Bürkner 2017) to independently model the relationship between each morphological measure – straight carapace length, carapace width, gape size, and body mass – and Blüthgen's d' as well as partner diversity, since normalized degree was only statistically significant for two tortoises in the full network after correcting for multiple comparisons, each tortoise having an opposing effect on normalized degree.

The model for Blüthgen's d' followed a beta error distribution and the model for partner diversity followed a gaussian error distribution. Both models employed the default uninformative prior distributions from the brms package. Afterward, I implemented model selection via Leave One Out Cross Validation (LOO-CV) from the loo R package (Vehtari et al. 2017), to select the leading model that best explained measures of Blüthgen's d' and partner diversity. Due to strong correlations between morphological traits, I only selected the top model for each network index to examine the influence morphology on network specialization. I then calculated the variance inflation factors of Blüthgen's d' and partner diversity and confirmed that these indices did not demonstrate signs of multicollinearity by having a variance inflation factor of 1.50. This value is much lower than the 5.00 threshold that alludes to issues with multicollinearity.

After selecting the leading models for Blüthgen's d' and partner diversity, I extracted the median slope estimates, lower and upper 95% Credible Intervals, R^2 values, and the probability of direction (PD) for the slope of each model. PD is defined as the probability that the relationship is in the direction of the median posterior estimate, and is

frequently used in Bayesian statistics as a measure of certainty for the modeled effect (Makowski et al. 2019).

3.4.5. Interaction Dissimilarity Between Wet and Dry Season Subnetworks

To quantify how the wet and dry season subnetworks differ in their structure and connections, I first calculated the interaction dissimilarity (β_{WN}) between the two subnetworks following the approach of Vizentin-Bugoni et al. (2019) in the `betalinkr` package (Fründ 2021). Interaction dissimilarity calculates what proportion of the connections in the two networks are different from one another and further identifies how much of the observed difference is due to species turnover processes (β_{ST}) or network rewiring (β_{OS}).

Species turnover is the emergence/disappearance of species that are present in one network but not in the other whereas rewiring is – as the name suggests – the reorganization of links between species/individuals found in both of the networks being compared (Poisot et al. 2012). The total interaction dissimilarity is then calculated as: $\beta_{WN} = \beta_{ST} + \beta_{OS}$ (Poisot et al. 2012, Fründ 2021). Once I calculated the total interaction dissimilarity and decomposed the contributions of species turnover and network rewiring, I then plotted both in a barchart and examined their relative contributions to the total observed interaction dissimilarity.

3.4.6. Contribution of Individuals and Fleshy Fruits to Interaction Dissimilarity

To test if interaction dissimilarity between seasons may be driven by the tortoises becoming more generalized in their seed dispersal interactions and by fleshy fruit (i.e.,

endozoochorous syndrome; Ridley 1930, Van der Pijl 1982) species becoming more integrated in the network as well, I performed GLMMs in the brms package (Bürkner 2017). I compiled the node-level indices, Blüthgen's d' and partner diversity, for the tortoise individuals and all plant species in the wet season and dry season subnetworks.

We then performed one GLMM for the higher-level nodes of the bipartite network – concerning the tortoises – to test for the effect of seasonality on Blüthgen's d' and partner diversity, while specifying a random effect to control for the individual tortoise effect. For plant species, I performed a similar GLMM but including an interaction term between the season (wet or dry) and the dispersal syndrome of the plant species (either the “endozoochorous” syndrome or “other”) while again accounting for differences among species by specifying a random effect for the species.

After running the model, I extracted the posterior estimates for the effects of seasonality on both tortoise network specialization (Blüthgen's d') as well as partner diversity. For the plant species, I also examined the effect of plants having the endozoochory dispersal syndrome on network specialization and partner diversity as well as its interaction with seasonality. The resulting estimates were plotted as a boxplot with the posterior median estimate and the standard errors for the estimate.

RESULTS

In total, the full seed dispersal network included 14 individual tortoises while the seasonal subnetworks each contained nine. I found that the tortoises dispersed seeds of 55 plant species in the full network, 29 in the dry season subnetwork, and 48 in the wet season subnetwork. The full network contained 442 interactions while the dry and wet

season subnetworks recorded 111 and 266 interactions, respectively (Table III.1). None of the networks were nested (wNODF) while only the seasonal subnetworks were more connected than expected by chance, probably because of their smaller size compared to the full network. Lastly, all three networks were more specialized (H2') and modular (Qw) than the 1000 vaznull networks they were each compared to (Table III.1). While the full network was not nested, it was indeed modular with 5 distinct modules (Fig. III.1). One of these modules – as suspected – only contained individuals from the East site, where many invasive plant species are found. In this module alone, more than 60% of the invasive plant species ($n = 8$) recovered from fecal samples were found to interact with the tortoises.

Calculating node-level indices for the individuals in the full network revealed that only Blüthgen's d' and partner diversity were significant and in the same direction for multiple individuals (Table III.2). The subsequent Generalized Linear Mixed Models (GLMMs) and LOO-CV model selection process resulted in the elimination of all other morphological traits besides carapace length (Table III.3), which best explained both node-level specialization as well as partner diversity. The GLMMs demonstrated that as carapace length increases, interaction specialization decreases and partner diversity increases (Fig. III.2). The median posterior estimates for the effect of carapace length on Blüthgen's d' and partner diversity were -0.07, and 0.04 respectively. For Blüthgen's d' , the lower and upper 95% Credible Interval values were -0.11 and -0.02 with an R^2 of 0.79 and a PD of 99.26%. For partner diversity, the lower and upper 95% Credible Interval estimates were -0.01 and 0.09, respectively, with an R^2 of 0.51 and a PD of 93.54%. Both models demonstrate a strong to moderately strong relationship between

carapace length and both node-level interaction specialization and partner diversity among individuals, after accounting for individual-level variation in other traits.

For the seasonal subnetworks, I found that both were significantly modular like the full network (Table III.1), each also containing five modules. To examine whether and how these two networks were dissimilar, I calculated the interaction dissimilarity between the two. This resulted in a β_{WN} value of 0.61, where 0.54 (89%) of the dissimilarity was driven by rewiring (β_{OS}) and 0.07 (11%) was driven by species turnover (β_{ST}) (Fig. III.3). Since I suspected that fleshy fruits drove seasonal patterns of seed dispersal, I color-coded fleshy fruit species in both seasonal subnetworks (Fig. III.4). This revealed that in the dry season, only four fleshy fruit species were dispersed whereas in the wet season there were 16. However, the fact that rewiring drove interaction dissimilarity led us to note that saw palmetto (*Serenoa repens*), eastern prickly pear (*Opuntia austrina*), and shrub verbena (*Lantana camara*) were among the plants least interacted with in the dry season – each only interacting with one individual – while in the wet season, these plants interacted with six, five, and three individuals, respectively.

To further investigate how seasonality and fleshy fruits may drive the observed interaction dissimilarity, I modeled the node-level measures of Blüthgen's d' and partner diversity for all plant species based on an interaction term between seasonality and dispersal syndrome while accounting for species-level differences. At the individual tortoise level, I ran a similar model specification for both node-level indices but with seasonality as the only predictor and individual tortoise differences accounted for through a random effect. These analyses revealed that seasonally, the gopher tortoises in this study became less specialized in their seed dispersal interactions in the wet season and

had a greater diversity of partners in the wet season than dry season – with estimates for both indices having a PD > 95% (Table III.4; Fig. III.5). Plants exhibiting the endozoochory syndrome demonstrated strong seasonal differences in both node-level specialization (Blüthgen's d') and partner diversity, with all estimates also having a PD value > 95% (Table III.4). This indicated that specialization was also lower and partner diversity was also higher for fleshy fruits in the wet season than dry season. While even for non-endozoochorous species there was less specialization in the wet season than dry season (Fig. III.5, panel c), the magnitude of this difference was much more pronounced for endozoochorous plants. These results revealed that indeed, seasonal differences in network structure are driven by node-level differences in network specialization and partner diversity – both across tortoises and the fleshy-fruited plant species whose seeds they disperse.

DISCUSSION

In this study, I characterized the structure and emergent properties of an intraspecific seed dispersal network. Specifically, I found that this network was not nested, but was indeed specialized and modular in its interactions. In addition to identifying network-wide patterns of specialization and modularity, I calculated node-level indices that captured how interaction specialization – as measured by Blüthgen's d' (Blüthgen et al. 2006) – and partner diversity varied across individuals varying in body size. I found that carapace length had a strong relationship with both indices where larger individuals were more generalized and more diverse in the partners they interacted with compared to smaller individuals, highlighting how intraspecific variation in

morphological traits influence the functional role of individuals as seed dispersers (Zwolak 2018, Zwolak and Sih 2020). More studies along this line of inquiry may identify other intraspecific traits that drive network patterns, highlighting the importance of conserving age/size classes, sexes, and behaviors that provide unique ecosystem services.

We subsequently found that the seasonal subnetworks were more modular and specialized than expected by chance alone, and further tested how these subnetworks differed from one another. Both subnetworks were considerably different largely due to network rewiring, which I confirmed was driven by increased generalization in the interactions of both gopher tortoise individuals as well as fleshy-fruited plant species in the pine rockland plant community. This aspect of the study stresses the important role of seasonal variation in mediating animal-plant seed dispersal interactions (Remis 1997, Koike et al. 2008, Yoshikawa and Osada 2015). The findings presented herein allude to an intra-annual shift along the mutualism-antagonism continuum by a generalist herbivore due to an increase in interactions with diverse fleshy-fruited plant species – subsequently dispersing their seeds and functionally behaving as a frugivore in the wet season (Marques Dracxler and Kissling 2022, van Leeuwen et al. 2022). This seasonal variation in seed dispersal interactions with fleshy fruits seemingly drives interaction dissimilarity between the wet and dry seasons.

In summary, by considering the life history and morphology of species, as well as the natural history of the communities in which they reside, individual-based seed dispersal networks could fundamentally change how seed dispersal ecological research is conducted and how it subsequently informs conservation and habitat management efforts.

One promising avenue for research is in tying theoretical concepts from niche theory, such as ecological opportunity and individual diet specialization to the study of seed dispersal networks (Bolnick et al. 2007, Araújo et al. 2011). By performing research that ties these two fields together, a more unified view of the role ecological opportunity plays in driving diet specialization – and subsequently interaction specialization – can shed light into the cascading ecological implications and how individuals may differ in their functional roles as seed dispersers (Bolnick et al. 2011, Zwolak 2018, Zwolak and Sih 2020). Importantly, studies of this scope should use the same categories to both calculate diet specialization and construct the subsequent seed dispersal networks to more seamlessly integrate these two subdisciplines of ecology.

TABLES

Seed Dispersal Network Descriptive Statistics			
Descriptor	All	Dry	Wet
# Tortoise Individuals	14	9	9
# Plant Species	55	30	50
# Links	197	68	123
# Interactions	442	111	266
Weighted Connectance	0.14 (0.13-0.14)	0.16 (0.13-0.14)	0.14 (0.11-0.13)
Specialization (H2')	0.30 (0.13-0.18)	0.41 (0.22-0.36)	0.32 (0.15-0.23)
Nestedness (wNODF)	20.91 (28.46-34.39)	14.06 (22.89-34.12)	19.27 (26.67-34.04)
Modularity (Qw)	0.28 (0.11-0.14)	0.34 (0.16-0.26)	0.27 (0.11-0.16)
# Modules	5	5	5
# Endozoochorous Species (%)	16 (29.09%)	5 (16.67%)	16 (32.00%)

Table III.1. Descriptive statistics for the three intraspecific seed dispersal networks, which indicate the number of tortoises, plant species, links, and interactions in each network, as well as the network-level indices for weighted connectance, specialization (H2'), nestedness (wNODF), and modularity (Qw).

Network	Node-Level Index	Node (Individual Tortoise)	Carapace Width (cm)	Observed Value	Lower.CL	Predicted	Upper.CL	SD	SES	p-value	Rank	Holm-Bonferroni alpha	(N.S. = not significant; * = < 0.05; ** = < 0.01; *** = < 0.001; **** = < 0.0001)
All (Weighted)	Blüthgen's d'	Ind.84	12.8	0.45	0.07	0.12	0.23	0.04	7.36	0.00000000	1	0.003571429	****
		Ind.615	15	0.37	0.07	0.12	0.22	0.04	6.07	0.00000000	2	0.003846154	****
		Ind.Scuteless	23.4	0.28	0.07	0.13	0.25	0.05	2.86	0.00211695	3	0.004166667	****
		Ind.490	17.6	0.37	0.07	0.13	0.27	0.05	4.44	0.00000458	4	0.004545455	****
		Ind.6000	17.8	0.28	0.07	0.11	0.21	0.04	4.29	0.00000879	5	0.005	****
		Ind.402	20.5	0.23	0.07	0.10	0.18	0.03	4.29	0.00000901	6	0.005555556	****
		Ind.606	25.1	0.33	0.07	0.13	0.26	0.05	4.21	0.00001278	7	0.00625	****
		Ind.454	20.7	0.24	0.07	0.11	0.20	0.03	3.80	0.00007143	8	0.007142857	****
		Ind.491	20.3	0.28	0.07	0.13	0.24	0.05	3.04	0.00117208	9	0.008333333	**
		Ind.40	21.6	0.19	0.06	0.10	0.19	0.03	2.86	0.00211695	10	0.01	**
		Ind.349	20	0.25	0.07	0.13	0.24	0.04	2.69	0.00353865	11	0.0135	**
		Ind.589	22.2	0.24	0.07	0.13	0.28	0.06	1.94	0.02630849	12	0.016666667	N.S.
		Ind.300	19.9	0.20	0.07	0.14	0.29	0.06	1.17	0.12178442	13	0.025	N.S.
		Ind.21	21.5	0.10	0.07	0.11	0.20	0.04	0.27	0.39537903	14	0.05	N.S.
All (Weighted)	Partner Diversity	Ind.40	21.6	2.92	1.92	2.28	2.53	0.15	4.25	0.00001075	1	0.003571429	****
		Ind.402	20.5	2.84	1.95	2.26	2.51	0.15	3.94	0.00004019	2	0.003846154	****
		Ind.454	20.7	2.78	1.77	2.17	2.47	0.17	3.51	0.00022483	3	0.004166667	****
		Ind.21	21.5	2.60	1.74	2.12	2.40	0.17	2.79	0.00261074	4	0.004545455	**
		Ind.589	22.2	2.23	1.33	1.82	2.21	0.23	1.78	0.03783633	5	0.005	N.S.
		Ind.Scuteless	23.4	2.28	1.69	2.11	2.40	0.18	0.91	0.18081218	7	0.00625	N.S.
		Ind.606	25.1	2.01	1.37	1.85	2.26	0.22	0.72	0.23549667	9	0.008333333	N.S.
		Ind.349	20	2.07	1.46	1.94	2.30	0.23	0.61	0.27115991	10	0.01	N.S.
		Ind.615	15	2.09	1.58	2.01	2.33	0.19	0.46	0.32182257	11	0.0125	N.S.
		Ind.490	17.6	1.89	1.31	1.84	2.22	0.25	0.20	0.42191499	12	0.016666667	N.S.
		Ind.300	19.9	1.78	1.12	1.73	2.15	0.26	0.12	0.45093248	13	0.025	N.S.
		Ind.491	20.3	1.90	1.34	1.88	2.24	0.22	0.07	0.47151017	14	0.05	N.S.
		Ind.84	12.8	1.82	1.53	1.99	2.33	0.21	-0.85	0.19742536	8	0.007142857	N.S.
		Ind.6000	17.8	1.82	1.62	2.07	2.37	0.20	-1.27	0.10192279	6	0.005555556	N.S.
All (Weighted)	Normalized Degree	Ind.40	21.6	0.49	0.25	0.35	0.44	0.05	2.88	0.00199491	1	0.003571429	**
		Ind.402	20.5	0.45	0.24	0.35	0.45	0.05	2.05	0.02029767	4	0.004545455	N.S.
		Ind.454	20.7	0.42	0.20	0.31	0.40	0.05	2.02	0.02153690	5	0.005	N.S.
		Ind.21	21.5	0.36	0.20	0.29	0.38	0.05	1.38	0.08308428	8	0.007142857	N.S.
		Ind.589	22.2	0.24	0.11	0.20	0.29	0.05	0.79	0.21587958	10	0.01	N.S.
		Ind.Scuteless	23.4	0.33	0.18	0.29	0.38	0.05	0.69	0.24522750	12	0.016666667	N.S.
		Ind.606	25.1	0.22	0.13	0.22	0.29	0.05	0.00	0.00000000	14	0.05	N.S.
		Ind.300	19.9	0.16	0.09	0.18	0.25	0.04	-0.42	0.33545126	13	0.025	N.S.
		Ind.491	20.3	0.18	0.13	0.22	0.31	0.05	-0.77	0.22177265	11	0.0125	N.S.
		Ind.349	20	0.18	0.15	0.24	0.33	0.05	-1.11	0.13375317	9	0.008333333	N.S.
		Ind.490	17.6	0.13	0.13	0.20	0.31	0.05	-1.62	0.05304794	7	0.00625	N.S.
		Ind.615	15	0.16	0.16	0.25	0.35	0.05	-1.87	0.03057898	6	0.005555556	N.S.
		Ind.84	12.8	0.13	0.15	0.24	0.35	0.05	-2.18	0.01479598	3	0.004166667	N.S.
		Ind.6000	17.8	0.13	0.16	0.27	0.36	0.05	-2.84	0.00228030	2	0.003846154	**

Table III.2. Summary table for node-level indices (Blüthgen's d', partner diversity, and normalized degree) calculated for individuals in the full network. Predicted null values, lower and upper confidence levels (CL), standard deviations (SD), standardized effect sizes (SES), p-values, significance rank, and Holm-Bonferroni alpha levels are all included. Rows are ordered in descending order of SES per index. The individual tortoise's identifier is included to keep track of each individual's estimated node-level index value. Significant results after Holm-Bonferroni correction are marked with an asterisk and highlighted in yellow.

Model	Node-Level Index	Morphological Trait	elpd_diff	se_diff
d.cl.glm	Blüthgen's d'	Carapace Length	0	0
d.gape.glm	Blüthgen's d'	Gape Size	-1.1	1.7
d.cw.glm	Blüthgen's d'	Carapace Width	-1.2	0.9
d.mass.glm	Blüthgen's d'	Body Mass	-2.1	1.1
partner.diversity.cl.glm	Partner Diversity	Carapace Length	0	0
partner.diversity.gape.glm	Partner Diversity	Gape Size	-0.3	0.5
partner.diversity.cw.glm	Partner Diversity	Carapace Width	-0.4	0.4
partner.diversity.mass.glm	Partner Diversity	Body Mass	-0.6	0.6

Table III.3. Leave One Out Cross Validation (LOO-CV) summary table showing the competing models for Blüthgen's d' and partner diversity, ordered from lowest difference in expected log pointwise predictive density (elpd_diff) to highest, along with the standard error for the difference (se_diff).

Network Level	Metric	Variable	Lower 95% CI	Median Estimate	Upper 95% CI	PD
Higher (Individual Tortoises)	Blüthgen's d'	Wet Season	-0.6	-0.39	-0.17	99.92%
Higher (Individual Tortoises)	Partner Diversity	Wet Season	0	0.42	0.85	97.32%
Lower (Plant Species)	Blüthgen's d'	Endozoochory Syndrome	0.12	0.58	1.04	99.39%
Lower (Plant Species)	Blüthgen's d'	Wet Season	-0.46	-0.25	-0.02	98.46%
Lower (Plant Species)	Blüthgen's d'	Endozoochory Syndrome:Wet Season	-1.08	-0.6	-0.12	99.21%
Lower (Plant Species)	Partner Diversity	Syndrome	-1.12	-0.510	0.07	95.76%
Lower (Plant Species)	Partner Diversity	Wet Season	-0.27	0.02	0.31	56.92%
Lower (Plant Species)	Partner Diversity	Endozoochory Syndrome:Wet Season	-0.06	0.57	1.19	96.08%

Table III.4. Generalized Linear Mixed Model (GLMM) summary table for the effect of seasonality on node-level measures of specialization (Blüthgen's d') and partner diversity for the tortoises in the population and plant species in the community. For the plant species, I interacted seasonality with dispersal syndrome. The reference level for comparing seasonal effects was the Dry season and for dispersal syndrome the reference level was the "Other" category, encompassing all other dispersal syndromes aside from endozoochory. Estimates for Blüthgen's d' are in log-odds. The lower 95% Credible Interval (CI), median estimate, upper 95% Credible Interval, and Probability of Direction (PD) are all included.

FIGURES

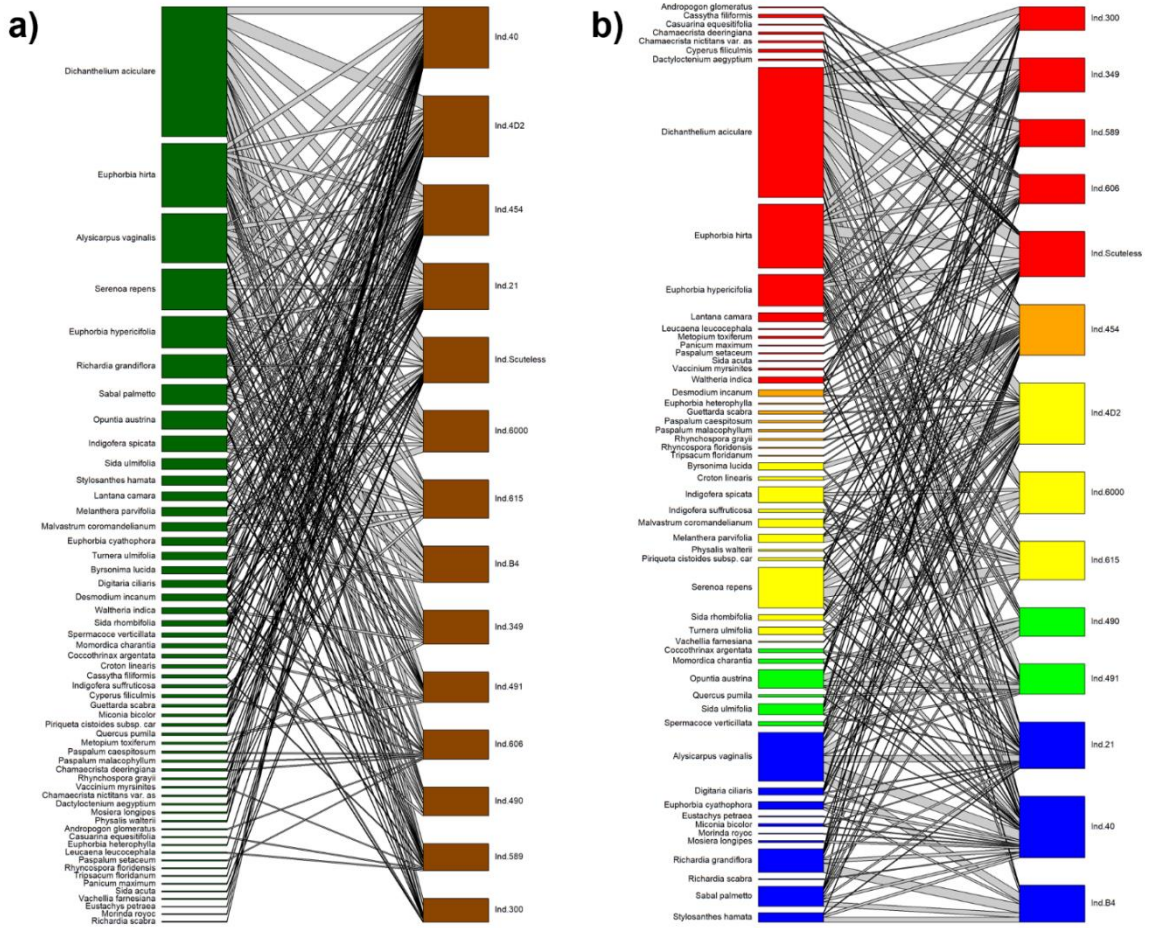


Figure III.2. Full intraspecific seed dispersal network illustrating interactions descending in intensity (panel a) and arranged in modules (panel b). a) Plant species are in dark green while individual gopher tortoises are in brown. b) All five modules present in the network are color-coded in red, orange, yellow, green, and blue.

Effect of Carapace Length (cm) on Network Specialization

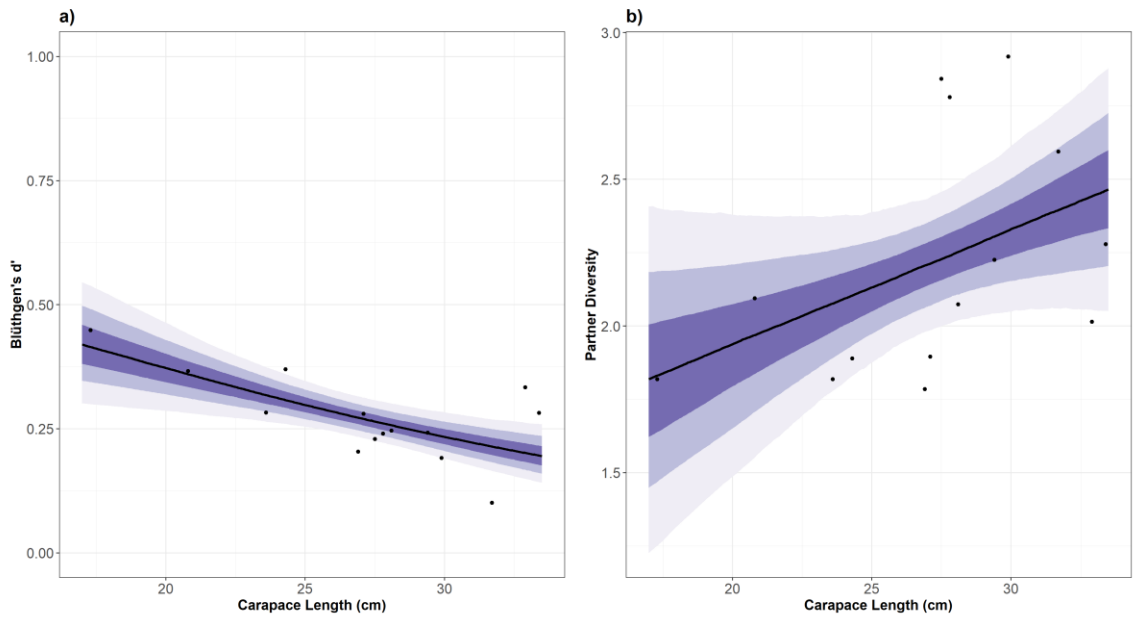


Figure III.3. Generalized Linear Mixed Models (GLMMs) illustrating the relationship between straight-line carapace length and Blüthgen's d' (vertical axis in panel a) and partner diversity (vertical axis in panel b).

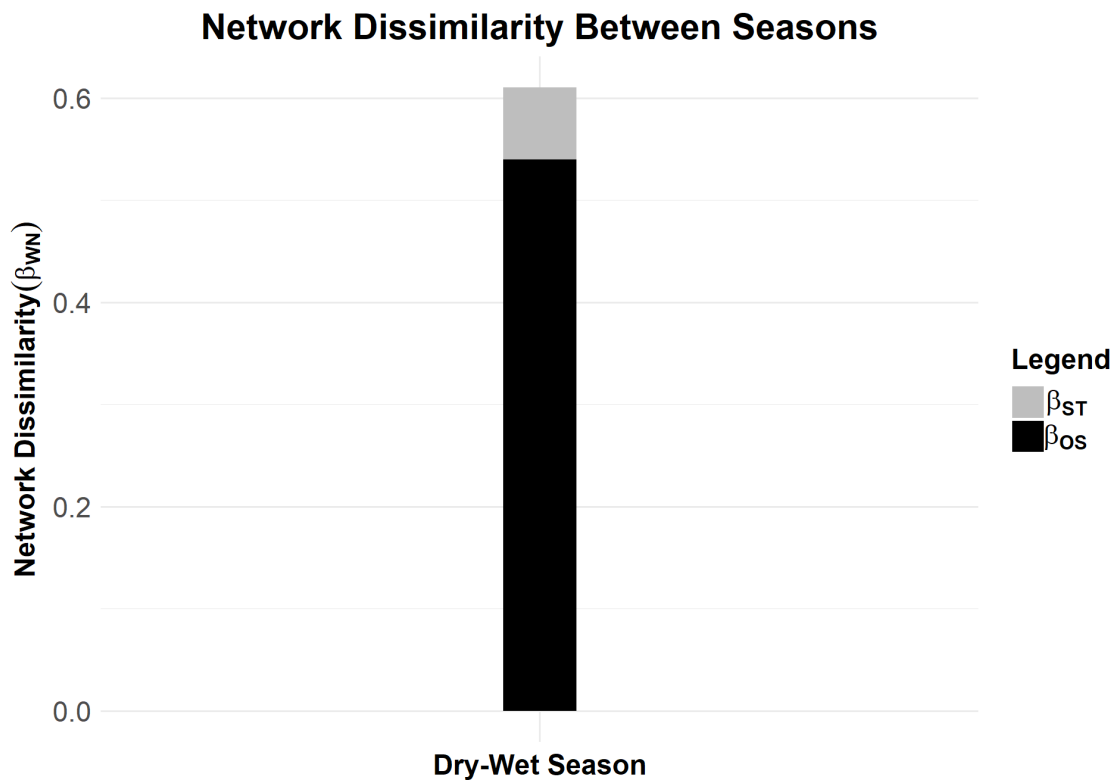


Figure III.4. Network dissimilarity between dry and wet season subnetworks. The black bar represents the contribution of rewiring (β_{OS}) to total network dissimilarity (β_{WN}) while the gray bar represents the contribution of species turnover (β_{ST}) to total network dissimilarity.

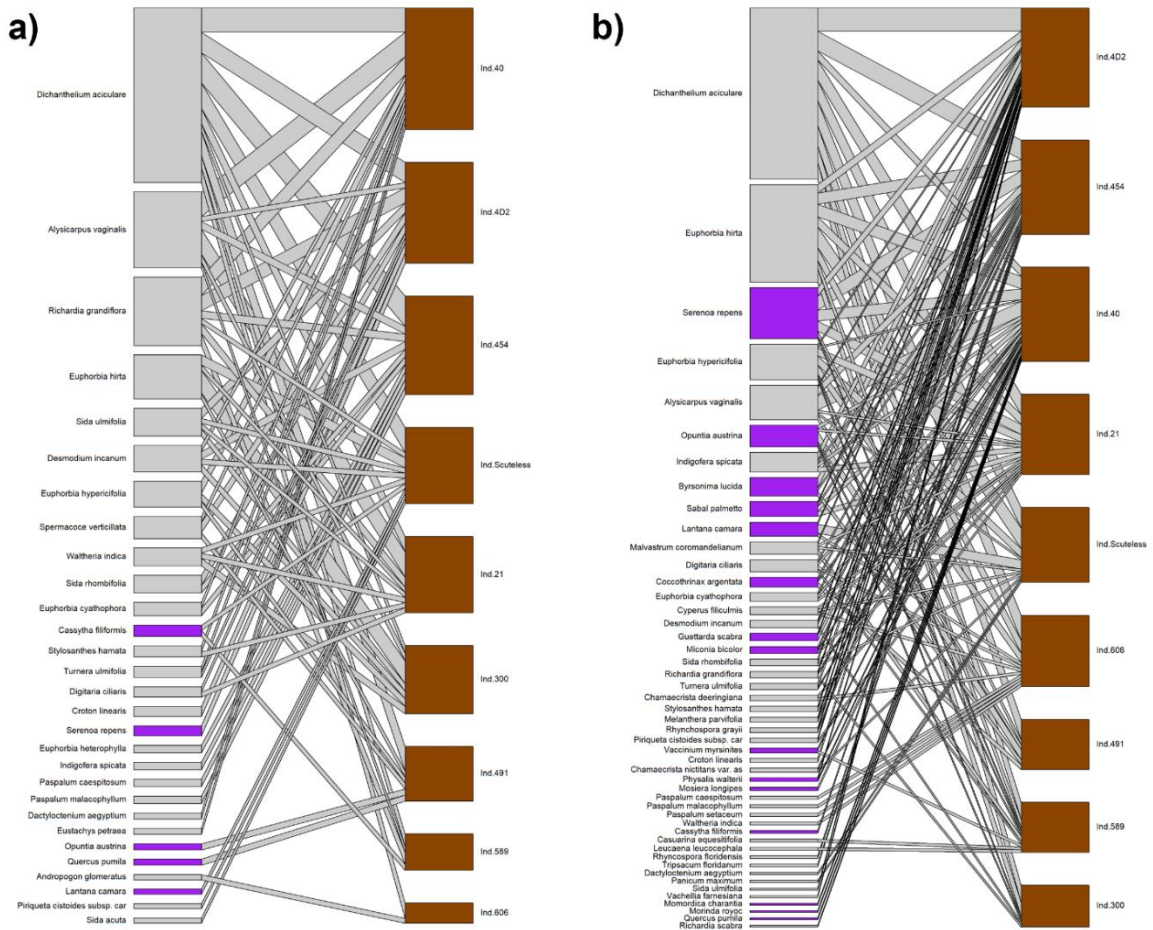


Figure III.5. Seasonal intraspecific seed dispersal subnetwork illustrating interactions descending in intensity in the dry season (panel a) wet season (panel b). In both panels, species with the endozoochory syndrome (fleshy fruit) are on the lefthand side of the network in purple while all other syndromes are in gray, and all individual tortoises are on the righthand side in brown.

Effect of Seasonality on Node-Level Indices for Tortoise Population (Top Row) and Plant Community (Bottom Row)

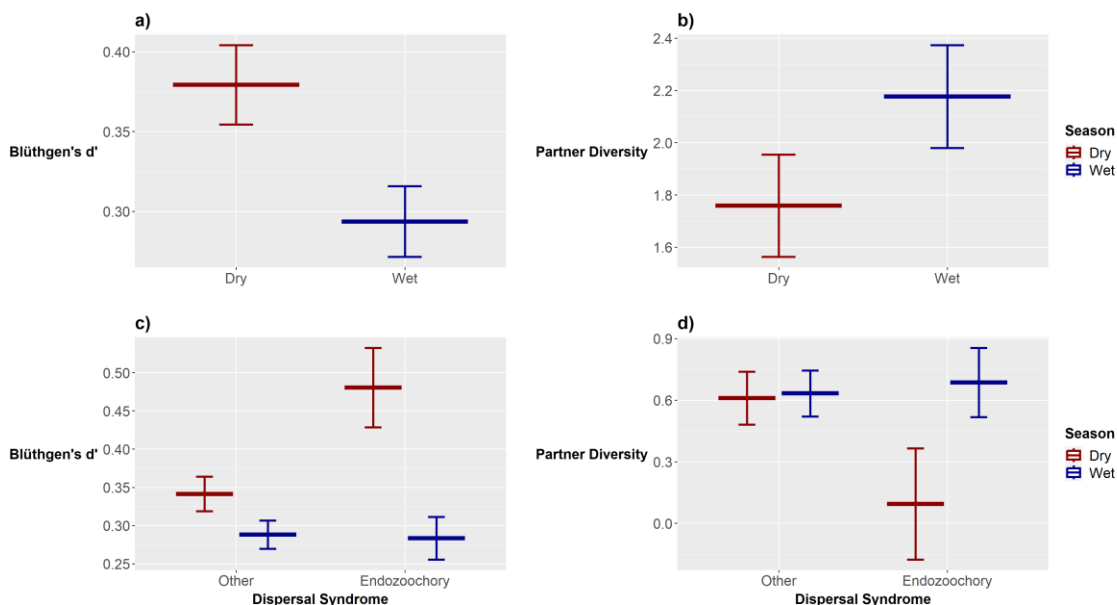


Figure III.6. Boxplots demonstrating the influence of seasonality on Blüthgen's d' and partner diversity in the tortoise population (panels a and b, respectively) and the plant community (panels c and d, respectively). The dry season is depicted in red in all plots and the wet season is depicted in blue. In panels c) and d), plants with the endozoochory syndrome are at the right-most extent of each panel and are labeled as such while plants with other seed dispersal syndromes are at the left-most extent of each panel and are also labeled.

LITERATURE CITED

- Almeida-Neto, M., P. Guimaraes, P. R. Guimaraes Jr, R. D. Loyola, and W. Ulrich. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117:1227–1239.
- Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. *Ecology Letters* 14:948–958.
- Armstrong, R. A. 2014. When to use the Bonferroni correction. *Ophthalmic and Physiological Optics* 34:502–508.
- Ashton, R. E., and P. S. Ashton. 2008. The Natural History and Management of the Gopher Tortoise. *Gopherus polyphemus*:65–93.
- Auffenberg, W., and R. Franz. 1978. *Gopherus polyphemus*. Catalogue of American Amphibians and Reptiles.
- Auffenberg, W., and R. Franz. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). *North American Tortoises: Conservation Ecology*:95–126.
- Balme, G. A., N. Roex, M. S. Rogan, and L. T. B. Hunter. 2020. Ecological opportunity drives individual dietary specialization in leopards. *Journal of Animal Ecology* 89:589–600.
- Bartel, S. L., and J. L. Orrock. 2022. The important role of animal social status in vertebrate seed dispersal. *Ecology Letters* 25:1094–1109.
- Bascompte, J. 2009. Mutualistic networks. *Frontiers in Ecology and the Environment* 7:429–436.
- Bascompte, J., and P. Jordano. 2007. Plant-animal mutualistic networks: The architecture of biodiversity. *Annual Review of Ecology Evolution and Systematics* 38:567–593.
- Bascompte, J., and P. Jordano. 2014. *Mutualistic Networks*. Princeton University Press.
- Bascompte, J., P. Jordano, C. J. Melián, and J. M. Olesen. 2003. The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences* 100:9383.
- Birkhead, R. D., C. Guyer, S. M. Hermann, and W. K. Michener. 2005. Patterns of folivory and seed ingestion by gopher tortoises (*Gopherus polyphemus*) in a southeastern pine savanna. *American Midland Naturalist* 154:143–151.
- Blüthgen, N., J. Fründ, D. P. Vázquez, and F. Menzel. 2008. What do interaction network metrics tell us about specialization and biological traits. *Ecology* 89:3387–3399.

- Blüthgen, N., F. Menzel, and N. Blüthgen. 2006. Measuring specialization in species interaction networks. *BMC Ecology* 6:9.
- Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution* 26:183–192.
- Bolnick, D. I., R. Svanbäck, M. S. Araújo, and L. Persson. 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences* 104:10075–10079.
- Bürkner, P.-C. 2017. brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software* 80:1–28.
- Carlson, J. E., E. S. Menges, and P. L. Marks. 2003. Seed dispersal by *Gopherus polyphemus* at Archbold Biological Station, Florida. *Florida Scientist* 66:147–154.
- Coblentz, K. E., A. E. Rosenblatt, and M. Novak. 2017. The application of Bayesian hierarchical models to quantify individual diet specialization. *Ecology* 98:1535–1547.
- Dennis, A. J. 2007. *Seed dispersal: theory and its application in a changing world*. CABI.
- Diamond, J. M., and J. T. Heinen. 2016. Conserving rare plants in locally-protected urban forest fragments: A case study from Miami-Dade County, Florida. *Urban Forestry & Urban Greening* 20:1–11.
- Diemer, J. E. 1986. The Ecology and Management of the Gopher Tortoise in the Southeastern United States. *Herpetologica* 42:125–133.
- Donatti, C. I., P. R. Guimarães, M. Galetti, M. A. Pizo, F. M. D. Marquitti, and R. Dirzo. 2011. Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecology Letters* 14:773–781.
- Dormann, C. F., J. Frund, N. Blüthgen, and B. Gruber. 2009. Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks. *The Open Ecology Journal* 2:7–24.
- Dormann, C. F., B. Gruber, and J. Fründ. 2008. Introducing the bipartite Package: Analysing Ecological Networks 8.
- Figueroa, A., J. T. Heinen, F. N. Ridgley, S. M. Whitfield, and H. Liu. 2023. Management of a Globally Imperiled and Fire-Dependent Ecosystem in the Urban Matrix of Miami-Dade County, Florida: A Case Study of the Richmond Tract Pine Rocklands. *Diversity* 15:426.

- Figueroa, A., J. Lange, and S. M. Whitfield. 2021. Seed Consumption by Gopher Tortoises (*Gopherus polyphemus*) in the Globally Imperiled Pine Rockland Ecosystem of Southern Florida, USA. *Chelonian Conservation and Biology* 20:27–34, 8.
- Flora of North America Editorial Committee, eds. 1993+. 2023. *Flora of North America North of Mexico* [Online]. New York and Oxford.
- Fründ, J. 2021. Dissimilarity of species interaction networks: how to partition rewiring and species turnover components. *Ecosphere* 12:e03653.
- Fuh, T., A. Todd, A. Feistner, G. Donati, and S. Masi. 2022. Group differences in feeding and diet composition of wild western gorillas. *Scientific Reports* 12:9569.
- Galetti, M., R. Guevara, M. C. Côrtes, R. Fadini, S. Von Matter, A. B. Leite, F. Labecca, T. Ribeiro, C. S. Carvalho, R. G. Collevatti, M. M. Pires, P. R. Guimarães, P. H. Brancalion, M. C. Ribeiro, and P. Jordano. 2013. Functional Extinction of Birds Drives Rapid Evolutionary Changes in Seed Size. *Science* 340:1086.
- Gann, G. D., C. G. Stocking, and Collaborators. 2001. Floristic Inventory of South Florida Database Online. The Institute for Regional Conservation. Delray Beach, Florida.
- Gann, G. D., S. W. Woodmansee, and K. A. Bradley. 2002. Rare plants of south Florida: their history, conservation and restoration. Institute for Regional Conservation.
- Gerardo Herrera M., L., C. Korine, T. H. Fleming, and Z. Arad. 2008. Dietary Implications of Intrapopulation Variation in Nitrogen Isotope Composition of an Old World Fruit Bat. *Journal of Mammalogy* 89:1184–1190.
- Gotelli, N. J., and D. J. McCabe. 2002. Species Co-Occurrence: A Meta-Analysis of J. M. Diamond's Assembly Rules Model. *Ecology* 83:2091–2096.
- Guyer, C., V. M. Johnson, and S. M. Hermann. 2012. Effects of Population Density On Patterns of Movement and Behavior of Gopher Tortoises (*Gopherus polyphemus*). *Herpetological Monographs* 26:122–134.
- Hanish, C. J. 2018. Seed Dispersal of the Cocoplum (*Chrysobalanus icaco*) by Gopher Tortoises (*Gopherus polyphemus*) in Southeastern Florida. Florida Atlantic University.
- Hoffmeister, J. E., K. W. Stockman, and H. G. Multer. 1967. Miami Limestone of Florida and its recent Bahamian counterpart. *Geological Society of America Bulletin* 78:175–190.
- Howe, H. F. 1986. CHAPTER 4 - Seed Dispersal by Fruit-Eating Birds and Mammals. Pages 123–189 in D. R. Murray, editor. *Seed Dispersal*. Academic Press, San Diego.

- Howe, H. F., and J. Smallwood. 1982. Ecology of Seed Dispersal. *Annual Review of Ecology and Systematics* 13:201–228.
- Jordano, P. 2016a. Chasing Ecological Interactions. *PLOS Biology* 14:e1002559.
- Jordano, P. 2016b. Sampling networks of ecological interactions. *Functional Ecology* 30:1883–1893.
- Jordano, P., and E. W. Schupp. 2000. Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* 70:591–615.
- Klein, P., and C. M. Smith. 2021. Invasive Johnsongrass, a threat to native grasslands and agriculture. *Biologia* 76:413–420.
- Koike, S., S. Kasai, K. Yamazaki, and K. Furubayashi. 2008. Fruit phenology of *Prunus jamasakura* and the feeding habit of the Asiatic black bear as a seed disperser. *Ecological Research* 23:385–392.
- van Leeuwen, C. H. A., N. Villar, I. Mendoza Sagrera, A. J. Green, E. S. Bakker, M. B. Soons, M. Galetti, P. A. Jansen, B. A. Nolet, and L. Santamaría. 2022. A seed dispersal effectiveness framework across the mutualism–antagonism continuum. *Oikos*:e09254.
- Levey, D. J., W. R. Silva, and M. Galetti. 2002. Seed dispersal and frugivory: ecology, evolution, and conservation. CABI.
- Lips, K. R. 1991. Vertebrates Associated with Tortoise (*Gopherus polyphemus*) Burrows in 4 Habitats in South-Central Florida. *Journal of Herpetology* 25:477–481.
- Lodge, T. E. 2017. *The Everglades Handbook: Understanding the Ecosystem (Fourth Edition)*. Everglades Handbook: Understanding the Ecosystem, 4th Edition.
- Makowski, D., M. S. Ben-Shachar, S. H. A. Chen, and D. Lüdecke. 2019. Indices of Effect Existence and Significance in the Bayesian Framework. *Frontiers in Psychology* 10:2767.
- Marques Dracxler, C., and W. D. Kissling. 2022. The mutualism–antagonism continuum in Neotropical palm–frugivore interactions: from interaction outcomes to ecosystem dynamics. *Biological Reviews* 97:527–553.
- Melanson, L. 2021. Investigating vertebrate relationships of the south Florida gopher tortoise: a study of vertebrate species within scrub, pine rockland, coastal hammock and grassland habitats. Florida Atlantic University.
- Monroe, M. B. 1943. Pioneer Women of Dade County. *Tequesta* 1:54–55.

- Mushinsky, H. R., T. A. Stilson, and E. D. McCoy. 2003. Diet and dietary preference of the juvenile gopher tortoise (*Gopherus polyphemus*). *Herpetologica* 59:475–483.
- Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15:278–285.
- Nathan, R., U. N. Safriel, I. Noy-Meir, and G. Schiller. 2000. Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. *Ecology* 81:2156–2169.
- Poisot, T., E. Canard, D. Mouillot, N. Mouquet, and D. Gravel. 2012. The dissimilarity of species interaction networks. *Ecology Letters* 15:1353–1361.
- Possley, J., J. Duncan, J. Klein, and J. Maguire. 2018. Miami-Dade County’s Management Plan for the Richmond Pine Rocklands, 2nd ed. Prepared by Fairchild Tropical Botanic Garden for Miami-Dade County, Department of Parks, Recreation and Open Spaces and Zoo Miami 2:136.
- Possley, J., S. W. Woodmansee, and J. Maschinski. 2008. Patterns of Plant Composition in Fragments of Globally Imperiled Pine Rockland Forest: Effects of Soil Type, Recent Fire Frequency, and Fragment Size. *Natural Areas Journal* 28:379–394.
- R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Remis, M. J. 1997. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: Use of variable resources. *American Journal of Primatology* 43:87–109.
- Richardson, J. C., and P. Stiling. 2019a. Gopher Tortoise (*Gopherus polyphemus*) Gut Passage Can Alter Seed Germinability. *The American Midland Naturalist* 182:181–190.
- Richardson, J. C., and P. Stiling. 2019b. Gopher tortoise herbivory increases plant species richness and diversity. *Plant Ecology* 220:383–391.
- Ridley, H. N. 1930. *The dispersal of plants throughout the world*. L. Reeve & Company, Limited.
- Rostal, D. C., E. D. McCoy, and H. R. Mushinsky. 2014. *Biology and conservation of North American tortoises*. JHU Press.
- Schupp, E. W. 1993. Quantity, Quality and the Effectiveness of Seed Dispersal by Animals. *Vegetatio* 108:15–29.
- Schupp, E. W., P. Jordano, and J. M. Gómez. 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist* 188:333–353.

- Simpson, C. T. 1920. In lower Florida wilds:174–184.
- Snyder, J. R. 1991. Fire regimes in subtropical south Florida. Pages 303–319.
- Snyder, J. R., A. Herndon, and W. B. Robertson Jr. 1990. South Florida Rockland. *Ecosystems of Florida*:230–277.
- Traveset, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics* 1:151–190.
- Traveset, A., R. Heleno, and M. Nogales. 2014. The Ecology of Seed Dispersal. *Seeds: The Ecology of Regeneration in Plant Communities*, 3rd Edition:62–93.
- Traveset, A., A. W. Robertson, and J. Rodríguez-Pérez. 2007. A review on the role of endozoochory in seed germination. Pages 78–103 in A. J. Dennis, E. W. Schupp, R. J. Green, and D. A. Westcott, editors. *Seed dispersal: theory and its application in a changing world*. First edition. CABI, UK.
- Trotta, L. B., B. Baiser, J. Possley, D. J. Li, J. Lange, S. Martin, and E. B. Sessa. 2018. Community phylogeny of the globally critically imperiled pine rockland ecosystem. *American Journal of Botany* 105:1735–1747.
- Van der Pijl, L. 1982. *Principles of dispersal in higher plants*. Springer.
- Vázquez, D. P., N. Blüthgen, L. Cagnolo, and N. P. Chacoff. 2009. Uniting pattern and process in plant–animal mutualistic networks: a review. *Annals of Botany* 103:1445–1457.
- Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing* 27:1413–1432.
- Vizentin-Bugoni, J., J. H. Sperry, J. P. Kelley, J. M. Gleditsch, J. T. Foster, D. R. Drake, A. M. Hruska, R. C. Wilcox, S. B. Case, and C. E. Tarwater. 2021. Ecological correlates of species' roles in highly invaded seed dispersal networks. *Proceedings of the National Academy of Sciences* 118:e2009532118.
- Vizentin-Bugoni, J., C. E. Tarwater, J. T. Foster, D. R. Drake, J. M. Gleditsch, A. M. Hruska, J. P. Kelley, and J. H. Sperry. 2019. Structure, spatial dynamics, and stability of novel seed dispersal mutualistic networks in Hawai'i. *Science* 364:78–82.
- Wenny, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research* 3:37–50.
- Whitfield, S. M., D. Valle, A. Figueroa, B. Chin, H. Bravo-Gallegos, and F. Leone. 2022. Burrow Characteristics and Habitat Associations of Gopher Tortoises in Urban

Pine Rockland Reserves (Miami, Florida, USA). *Ichthyology & Herpetology* 110:22–32.

World Wildlife Fund. 2014. South Florida rocklands.

Wunderlin, R. P., B. F. Hansen, A. R. Franck, and F. B. Essig. 2016. Atlas of Florida vascular plants. *Atlas of Florida vascular plants*.

Yoshikawa, T., and Y. Osada. 2015. Dietary Compositions and Their Seasonal Shifts in Japanese Resident Birds, Estimated from the Analysis of Volunteer Monitoring Data. *PLOS ONE* 10:e0119324.

Zwolak, R. 2018. How intraspecific variation in seed-dispersing animals matters for plants. *Biological Reviews* 93:897–913.

Zwolak, R., and A. Sih. 2020. Animal personalities and seed dispersal: A conceptual review. *Functional Ecology* 34:1294–1310.

CONCLUSION

In this dissertation, I have demonstrated intra-annual variation in diet specialization in the two distinct south Florida seasons: the wet season and the dry season. Previous research on desert tortoises (*Gopherus agassizii*) – a congener of the gopher tortoise (*Gopherus polyphemus*) – has shown that there is greater diet specialization as precipitation increases (Murray and Wolf 2013), which I corroborate here using traditional indices of individual diet specialization from the niche theory literature (Bolnick et al. 2002, Araújo et al. 2011, Coblenz et al. 2017). I showed that not only is there a seasonal difference in diet specialization across the population, but that at the individual-level gopher tortoises demonstrate varying levels of consistency in their own diets as well as in their specialization when compared to the whole population.

Furthermore, not only did individuals become more specialized in the wet season compared to the dry season, but their dietary composition shifted toward a more frugivorous one – a foraging habit that has been documented in another hindgut fermenter (Bjorndal 1987, Remis and Dierenfeld 2004), the western lowland gorilla (*Gorilla gorilla gorilla*) (Remis 1997). To test if frugivory was what drove diet consistency and specialization, I modeled how these two indices of diet specialization changed as the proportion of fecal volume comprised of fruit increased, and found a strong relationship which confirmed that frugivory, in fact, allows the gopher tortoise to specialize on a more unique subset of resources when compared to the rest of the population. I believe this phenomenon is alluding to the notion that as ecological opportunity increases (Araújo et al. 2011, Balme et al. 2020) – via changes in fruit availability due to the phenology of south Florida plant species (Flora of North America

Editorial Committee, eds. 1993+ 2023) – so does the degree of individual diet specialization in the gopher tortoise. This shift toward a more specialized diet as fruit availability increases has been demonstrated in fruit bats (Gerardo Herrera M. et al. 2008), and many species are known to track the temporal availability of fleshy fruit resources (Koike et al. 2008, Robira et al. 2023).

To better characterize how fruit consumption changed over the course of the study, I modelled the proportion of fecal volume made of fruit as a function of the calendar day through a Generalized Additive Mixed Model (GAMM) (Pedersen et al. 2019). This revealed a very strong seasonal pattern that coincided with precipitation. Due to the time lags between precipitation falling, flowers developing and turning into ripe fruit, and subsequently appearing in the fecal samples, we observed that frugivory increased after seasonal rains were at its highest (between June and November). The Generalized Linear Mixed Model (GLMM) I performed revealed that this pattern of frugivory was clearly defined, ranging from very low levels of frugivory in the winter and spring that increased drastically in the summer and subsequently decreased throughout the fall.

I then narrowed down the subset of the 16 fleshy-fruited plant species that best explained the gopher tortoise fruit diet. This narrowed the list to five species: saw palmetto (*Serenoa repens*), silver palm (*Coccothrinax argentata*), sabal palm (*Sabal palmetto*), eastern prickly pear (*Opuntia austrina*), and locustberry (*Byrsonima lucida*). These five species captured >95% of the frugivory in the gopher tortoises studied here. However, considering the diversity of fleshy fruits the tortoises consumed as well as the temporally cyclical pattern of frugivory, I ran another GLMM but this time to see if as

frugivory increased, did the dispersal of different species with fleshy fruits. This analysis revealed that indeed as fruit consumption increased, so did the dispersal of seeds for fleshy-fruit-bearing plant species. These results demonstrated that the functional role of the gopher tortoise seems to change as they become more frugivorous, potentially behaving more like a frugivore than a folivore (van Leeuwen et al. 2022).

After gaining insight into the temporal patterns of frugivory and its implications for seed dispersal of fleshy fruited species, I decided to use an ecological network approach to quantify first, how intraspecific seed disperser networks are structured, which individual morphological trait best explained interaction specialization of individuals, how seasonality influenced network connections, and whether the endozoochory syndrome (i.e., fleshy fruit; Ridley 1930, Van der Pijl 1982) contributed to interaction dissimilarity between the wet season and dry season subnetworks. I found that the full seed dispersal network – containing all individuals from the population that provided more than 4 fecal samples – was more specialized and modular than null predictions. I subsequently modeled node-level indices of specialization as a function of different individual-specific morphological traits, of which I found carapace length was the best predictor for both interaction specialization as well as partner diversity, where larger tortoises were more generalized in their interactions and had a greater diversity of partners than smaller tortoises.

I then found that between the wet season and dry season, networks were very dissimilar, mainly due to rewiring rather than species turnover between the networks. To better understand how rewiring may have been driven by interaction specialization and partner diversity, I modeled the influence of dispersal syndrome and seasonality on both

node-level measures for the lower level (i.e., plant species) of the network, while I separately modeled the role of seasonality on the same node-level measures for the upper level of the network (i.e., individual tortoises). This exercise revealed that seasonality and the endozoochory syndrome drove patterns of interaction specialization as well as partner diversity, where in the wet season interactions were much more generalized both for the tortoise individuals and the plant species – in particular the endozoochorous species. In this same vein, I found that partner diversity also increased for the tortoises and the endozoochorous plant species in the wet season compared to the dry season.

In all, these results demonstrated that larger tortoises tend to be more generalized in their interactions and interact with a greater diversity of plant species, whose seeds they disperse. Seasonally, the wet season subnetwork was different than the dry season subnetwork due to network rewiring, which I found was driven both by increased generalization in the interactions of the tortoises, as well as an increase in their partner diversity – which was also the case particularly with endozoochorous plant species.

The culmination of this dissertation is to highlight the important influence of temporal factors – specifically seasonal patterns of rain and fruiting phenology (Lodge 2017, Flora of North America Editorial Committee, eds. 1993+ 2023) – on the degree of diet specialization even in a mega generalist herbivore like the gopher tortoise (Ashton and Ashton 2008). Although not quantified in this body of work, the likely underlying explanation is an increase in fruit resource availability (i.e., ecological opportunity; Araújo et al. 2011). I suspect that seasonal pulses of rain result bring with them an increase in fruit availability which the gopher tortoises exploit, as evidenced in their temporally cyclical pattern of frugivory, fundamentally changing their functional role as

seed dispersers as I revealed in Chapter 3. This body of work illustrates a shift along the mutualism-antagonism continuum by the gopher tortoise (Marques Dracxler and Kissling 2022, van Leeuwen et al. 2022), where it ecologically functions as a frugivore by dispersing a great diversity of plant species – specifically fleshy fruited species during periods of high frugivory (i.e., the wet season).

By focusing on conspecifics rather than different species, I further demonstrated the importance of individuality in mediating seed dispersal interactions (Zwolak 2018, Zwolak and Sih 2020), specifically by analyzing the influence of morphological traits on node-level indices of interaction specialization for the gopher tortoise. Rather than focusing solely on differences in seed dispersal effectiveness between species (sensu Schupp 1993, Schupp et al. 2010), studies that quantify how individuals of the same species differ in their roles as frugivores and seed dispersers can provide new insights into the consequences of intraspecific trait variation for seed dispersal (Bolnick et al. 2011, Zwolak 2018, Zwolak and Sih 2020).

An exciting avenue for future research is in linking niche theory – particularly individual diet specialization – to network theory in the study of seed dispersal interactions as well as potentially plant-pollinator, predator-prey, and host-parasite interactions. This direction of research may allow researchers to quantify whether dietary specialists in a population also provide unique ecosystem services. Additionally, carefully quantifying how ecological opportunity varies spatiotemporally can demonstrate how this driver of diet specialization may also facilitate spatial and temporal variation in frugivory and seed dispersal services provided by populations of dispersers for surrounding plant communities (Araújo et al. 2011).

A final suggestion for future studies is to further explore the seed dispersal services provided by animals to non-fleshy fruits. Previous research has shown that dispersal syndromes alone are not reliable in predicting dispersal via ingestion and excretion through the animals (Green et al. 2021), and gopher tortoises in particular are known to forage on and disperse the seeds of many non-fleshy fruited species (Carlson et al. 2003, Birkhead et al. 2005, Figueroa et al. 2021). Research on potential tradeoffs and intraguild competition for seed dispersal services provides an interesting avenue for future research – especially in the case of herbivores where the foliage of vegetation they consume can ecologically function as the fruit (Janzen 1984).

LITERATURE CITED

- Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. *Ecology Letters* 14:948–958.
- Ashton, R. E., and P. S. Ashton. 2008. The Natural History and Management of the Gopher Tortoise. *Gopherus polyphemus*:65–93.
- Balme, G. A., N. Roex, M. S. Rogan, and L. T. B. Hunter. 2020. Ecological opportunity drives individual dietary specialization in leopards. *Journal of Animal Ecology* 89:589–600.
- Birkhead, R. D., C. Guyer, S. M. Hermann, and W. K. Michener. 2005. Patterns of folivory and seed ingestion by gopher tortoises (*Gopherus polyphemus*) in a southeastern pine savanna. *American Midland Naturalist* 154:143–151.
- Bjorndal, K. A. 1987. Digestive Efficiency in a Temperate Herbivorous Reptile, *Gopherus polyphemus*. *Copeia* 1987:714–720.
- Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution* 26:183–192.
- Bolnick, D. I., L. H. Yang, J. A. Fordyce, J. M. Davis, and R. Svanbäck. 2002. Measuring Individual-Level Resource Specialization. *Ecology* 83:2936–2941.

- Carlson, J. E., E. S. Menges, and P. L. Marks. 2003. Seed dispersal by *Gopherus polyphemus* at Archbold Biological Station, Florida. *Florida Scientist* 66:147–154.
- Coblentz, K. E., A. E. Rosenblatt, and M. Novak. 2017. The application of Bayesian hierarchical models to quantify individual diet specialization. *Ecology* 98:1535–1547.
- Figuroa, A., J. Lange, and S. M. Whitfield. 2021. Seed Consumption by Gopher Tortoises (*Gopherus polyphemus*) in the Globally Imperiled Pine Rockland Ecosystem of Southern Florida, USA. *Chelonian Conservation and Biology* 20:27–34, 8.
- Flora of North America Editorial Committee, eds. 1993+. 2023. *Flora of North America North of Mexico* [Online]. New York and Oxford.
- Gerardo Herrera M., L., C. Korine, T. H. Fleming, and Z. Arad. 2008. Dietary Implications of Intrapopulation Variation in Nitrogen Isotope Composition of an Old World Fruit Bat. *Journal of Mammalogy* 89:1184–1190.
- Green, A. J., C. Baltzinger, and Á. Lovas-Kiss. 2021. Plant dispersal syndromes are unreliable, especially for predicting zoochory and long-distance dispersal. *Oikos*.
- Janzen, D. H. 1984. Dispersal of Small Seeds by Big Herbivores: Foliage is the Fruit. *The American Naturalist* 123:338–353.
- Koike, S., S. Kasai, K. Yamazaki, and K. Furubayashi. 2008. Fruit phenology of *Prunus jamasakura* and the feeding habit of the Asiatic black bear as a seed disperser. *Ecological Research* 23:385–392.
- van Leeuwen, C. H. A., N. Villar, I. Mendoza Sagrera, A. J. Green, E. S. Bakker, M. B. Soons, M. Galetti, P. A. Jansen, B. A. Nolet, and L. Santamaría. 2022. A seed dispersal effectiveness framework across the mutualism–antagonism continuum. *Oikos*:e09254.
- Lodge, T. E. 2017. *The Everglades Handbook: Understanding the Ecosystem (Fourth Edition)*. *Everglades Handbook: Understanding the Ecosystem*, 4th Edition.
- Marques Dracxler, C., and W. D. Kissling. 2022. The mutualism–antagonism continuum in Neotropical palm–frugivore interactions: from interaction outcomes to ecosystem dynamics. *Biological Reviews* 97:527–553.
- Murray, I. W., and B. O. Wolf. 2013. Desert Tortoise (*Gopherus agassizii*) Dietary Specialization Decreases across a Precipitation Gradient. *Plos One* 8:e66505.
- Pedersen, E. J., D. L. Miller, G. L. Simpson, and N. Ross. 2019. Hierarchical generalized additive models in ecology: an introduction with mgcv. *PeerJ* 7:e6876.

- Remis, M. J. 1997. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: Use of variable resources. *American Journal of Primatology* 43:87–109.
- Remis, M. J., and E. S. Dierenfeld. 2004. Digesta Passage, Digestibility and Behavior in Captive Gorillas Under Two Dietary Regimens. *International Journal of Primatology* 25:825–845.
- Ridley, H. N. 1930. *The dispersal of plants throughout the world*. L. Reeve & Company, Limited.
- Robira, B., S. Benhamou, T. N. Fuh, and S. Masi. 2023. Do Seasonal Frugivory and Cognition Shape Foraging Movements in Wild Western Gorillas? Pages 151–170 in R. Reyna-Hurtado, C. A. Chapman, and M. Melletti, editors. *Movement Ecology of Afrotropical Forest Mammals*. Springer International Publishing, Cham.
- Schupp, E. W. 1993. Quantity, Quality and the Effectiveness of Seed Dispersal by Animals. *Vegetatio* 108:15–29.
- Schupp, E. W., P. Jordano, and J. M. Gómez. 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist* 188:333–353.
- Van der Pijl, L. 1982. *Principles of dispersal in higher plants*. Springer.
- Zwolak, R. 2018. How intraspecific variation in seed-dispersing animals matters for plants. *Biological Reviews* 93:897–913.
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- Figueroa, A., J. T. Heinen, F. N. Ridgley, S. M. Whitfield, and H. Liu. 2023. *Management of a Globally Imperiled and Fire-Dependent Ecosystem in the Urban Matrix of Miami–Dade County, Florida: A Case Study of the Richmond Tract Pine Rocklands*. Diversity 15:426.
- Whitfield, S. M., D. Valle, A. Figueroa, B. Chin, H. Bravo-Gallegos, and F. Leone. 2022. *Burrow Characteristics and Habitat Associations of Gopher Tortoises in Urban Pine Rockland Reserves (Miami, Florida, USA)*. Ichthyology & Herpetology 110:22-32.
- Figueroa, A., Lange, J., and Whitfield, S. M. 2021. *Seed Consumption by Gopher Tortoises (Gopherus polyphemus) in the Globally Imperiled Pine Rockland Ecosystem of Southern Florida, USA*. Chelonian Conservation and Biology, 20(1), 27-34, 28.